Russian Journal of Aquatic Ecology, 1(1), 1992, pp. 9-37

FISH IMPACT ON THE STRUCTURE, ABUNDANCE, AND BIOMASS OF PLANKTON AND BENTHOS OF TWO SMALL SHALLOW LAKES: A THREE-YEAR STUDY

A.F.ALIMOV, L.E.ANOKHINA, E.V.BALUSHKINA, S.M. GOLUBKOV, T.V.KHLEBOVICH, P.I.KRYLOV, E.B. PAVELJEVA, I.V.TELESH AND L.P.UMNOVA

Zoological Institute of Russian Academy of Sciences, Universitetskaya nab. 1, St.Petersburg 199034, Russia

Abstract. Structure, abundance and biomass dynamics of plankton and benthos in two small shallow neighbouring lakes during summer seasons 1986-1988 were compared. There were no fish in one of the lakes, Maly Okunyonok (MO) during 1986-1987; in 1988, it was stocked with carp fry. Different amounts of young planktivorous (*Coregonus peled*) and benthivorous (*Cyprinus carpio*) fish were also stocked in the other lake, Bolshoy Okunyonok (BO), during three years. Intensive pressure of planktivorous fishes altered greatly the zoo-, phyto- and bacterio-plankton structure. Small cyclopoid (*Thermocyclops, Mesocyclops*) and cladoceran (*Bosmina longirostris, Chydorus sphaericus, Daphnia galeata*) species prevailed in the zooplankton of BO. On the contrary, larger species (*Daphnia longispina* and *Chaoborus flavicans* larvae) dominated in the zooplankton of MO. *Asplanchna priodonta* played an important role among rotifers in BO whereas it was very rare in MO. Among Infusoria, the dominant group of plankton of both BO and MO, no common for these lakes species were found.

The percentage of bacteria associated with detritus particles was higher in BO. The summer phytoplankton bloom in MO was the result of *Anabaena spiroides* growth, while other species dominated in the BO phytoplankton. Benthivorous fishes dramatically affected the benthos biomass when the fish stock was high. Their pressure resulted also in alteration of the structure of benthos communities and led to a decline of the percentage of leeches in the total biomass of benthic animals.

During 1986-1987, the heavy fish pressure in BO resulted in a 19-65 fold decline of the mean seasonal biomass of *Chaoborus* larvae, and a 2.8-3.5 fold decline of planktonic crustaceans as compared to MO. Within the same period, in BO, the biomass of rotifers was 1.6 to 2.1 times higher, that of phytoplankton was 1.5 to 1.6 times higher, and the biomass of heterotrophic bacteria was 1.3-5.0 times higher than those in MO. Mean chlorophyll-a content in BO was 1.1 to 1.6 times higher while the water transparency (Secchi disc depth) was 1.3 to 1.9 times lower than in MO. An indirect effect of benthivorous fishes on pelagic food web components was inferred from observations in 1988. Possible mechanisms of the direct and mediated effects of fish on the plankton and benthos seasonal dynamics are discussed.

Key words: fish impact, plankton, benthos, top-down effects.

1. Introduction

Beginning from Hrbaček (Hrbaček 1962, Hrbaček et al. 1961) and Brooks and Dodson (1965), the emphasis in the recent limnology has been placed on "top-down" effects. This interest is explained to a great extent by the new possibilities of controlled influence on the structure of lake ecosystem and consequently by new means of eutrophication control instead of (or parallel to) well-known reduction of nutrient loading. In recent years, these methods of water quality improvement by changing the abundance and structure of fish populations were regarded as the biomanipulation and have been widely used in many countries (Shapiro 1980, Benndorf 1988a, van Donk and Gulati 1989, Gulati et al. 1990). Besides the applied aspect, the study of mechanisms of both the direct and indirect effects of predators on a community provides a new insight into the complex relationships between various components of aquatic ecosystems, and hence, a better understanding of their functioning (Kerfoot and Sih 1987, Carpenter 1988).

The main approach to the study of fish impact

on the lake ecosystem consists in the purposeful change of planktivorous or benthivorous predation. The reduction of fish abundance is achieved by removing fish from the lake, treatment of the lake with ichthyocides or stocking it with predatory fish. An opposite effect is observed in the cases of stocking the previously fish-free lakes, introduction of new species, limitations of catch, improvement of conditions for fish reproduction or reduction of the predatory fish populations (e.g. Benndorf 1988b, 1990). The effects of fish on various components of ecosystem may be revealed basing on limnological observations before and after the manipulation with fish pressure. Although this approach provides some useful information, it has certain limitations. As it is known, the annual fluctuations of community dynamics, caused by weather or other external factors, are frequently great. Therefore, a comparison of the results obtained in a lake in different years cannot always be related to a single factor.

Another less common approach consists in the comparison of similar closely located lakes with different fish densities (e.g. Carpenter et al. 1987, Elser and Carpenter 1988). In this case, one of two lakes may be treated as "control" and the other as "experimental". However, since there are no two absolutely identical lakes, the correctness of such a comparison is also open to question. A combination of both approaches seems to be the optimum solution.

The present paper concerns the first results of three year studies conducted in two small forest lakes during 1986-1988. These lakes, namely Bolshoi Okunyonok and Maly Okunyonok (referred below as BO and MO), are situated in the Luga district of the St.Petersburg region (58°50'N, 29°30'E). During the first two years, BO, devoid of aboriginal fish fauna, was stocked with larvae of peled *(Coregonus peled)* and other whitefishes (*Coregonus nasus*) as well as with fry of carp, *Cyprinus carpio*. In autumn, all the fishes were caught. For more details see the section "Area studied". MO, also devoid of fishes, was not stocked. Only few individuals from previous stockings were present. In 1988, BO was stocked as previously, and MO was also stocked with peled and carp. Although this attempt was not very successful (see below), some fishes were present. The main aim of fishery studies in these lakes was the determination of the optimum level of stocking to maximize fish production (see Table 1 in Benndorf 1990). However, studies conducted on the lakes during this period allowed to analyse the effects of fish on biotic communities. The lakes were compared according to the scheme: BO'86 — MO'86, BO'87 — MO'87, BO'88 — MO'88, and MO'88 — MO'86-87.

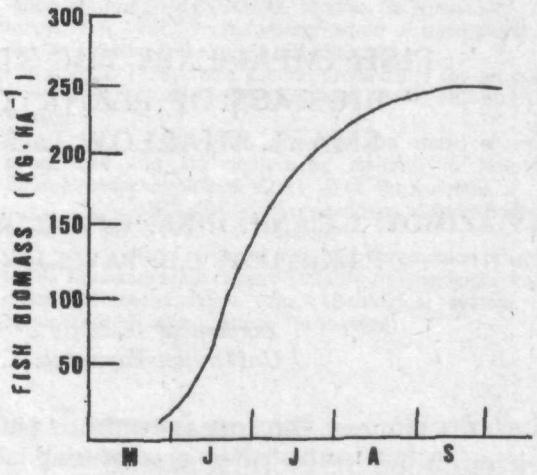

Fig. 1. Seasonal dynamics of the total fish biomass in BO during the summer of 1986 (from Rudenko et al. 1989).

According to the main aim of biomanipulation (namely, the reducing of phytoplankton development in water bodies), the research was usually focused on the "planktivorous fishes — zooplankton filtrators (crustaceans, rotifers) — phytoplankton" chain. As to heterotrophic bacteria and protozoans, their interrelations with other organisms were often ignored although these groups may play an important role in the trophic dynamics of pelagic lake communities (Stockner and Porter 1988). There are few studies that analyse simultaneously the effects of both planktivorous and benthivorous fish within the same ecosystem (Weglenska et al. 1979, Richardson et al. 1990). Another purpose of this paper was to combine the current concepts of top-down effects on phyto- and zooplankton with the data on responses of planktonic bacteria, heterotrophic protozoans, and zoobenthos.

2. Area studied

The water surface area of BO is 5.8 hectares, maximum depth 3 metres, mean depth 2 metres. The lake is fed by surface flow and precipitation. The water colour is yellowish brown. Higher aquatic vegetation is poorly developed.

Area of MO is 2.7 hectares, maximum depth 2 metres, mean depth 1.5 metres. The lake is fed by precipitation and to a great extent by flows from the bogs adjoining the lake. The water colour is dark brown.

Large part of low coastal zone (up to a depth of 2.0 — 2.3 m) in both BO and MO is occupied by brown mud, where peat and coarse detritus are predominant. This zone is also partially

Table 1. Results of fish rearing in BO and MO during 1986-1988 (Rudenko et al., 1989 and personal communication).

Lake, year	Fish, age	Date of Stocking	Stocking density, 10^3/ha	Body weight, g		Catch kg/ha	% survival	Final fish biomass, kg/ha
				Initial	Final			
BO' 1986	*Coregonus peled* (0+)	5 May	13.8	0.003	23.0	35.5	12.2	38.4
	Coregonus peled x *C. nasus* (0+)	5 May	13.8	0.003	20.0	44.5	18.1	46.4
	Cyprinus carpio (0+)	27 May	4.2	1.10	52.0	139.8	79.0	169.8
	C. carpio (1+, 2+)	From previous years				59.0	—	59.0
	Total					278.8	—	313.6
BO' 1987	*Coregonus peled* (0+)	19 May	12.4	0.003	18.7	82.6	59.5	138.1
	Cyprinus carpio (0+)	29 May	2.1	1.05	89.8	62.5	71.5	139.8
	Total					145.1	—	277.9
BO' 1988	*Coregonus peled* (0+)	14 May	8.1	0.003	17.9	86.0	60.0	87.1
	Cyprinus carpio (0+)	28 May	1.1	0.216	62.1	93.0	22.8	146.6
	C. carpio (0+)	21 June	0.9	0.165	161.7	13.1	13.5	21.4
	Total					192.1	—	255.1
MO' 1988	*Coregonus peled* (0+)	2 June	5.0	0.008	61.5	5.8	5.0	14.8
	Cyprinus carpio (0+)	28 May	0.37	0.216	710.0	95.0	60.5	151.2
	C. carpio (0+)	21 June	0.37	0.165	180.0	18.0	96.8	61.3
	Carassius auratus (1+,2+)	From previous years			1200.0	17.8	—	—
	Total					136.6	—	227.3

covered with muddy sands. There are abundant *Numphar luteum* (L.) in some places as well. Central parts of the lake hollows are 2.2-3.0 m deep in BO and 1.2-1.7 m in MO. They are covered with a thick layer of liquid brown mud and comprise the main part of these lake areas.

BO and MO are situated near each other, the minimum distance between them not exceeds 150 m. The lakes were previously connected by a narrow artificial canal. At present, the water exchange between the lakes occurs only in spring.

From the early 1970s, the regular observations were conducted on these and other lakes of Syaber group by the Hydrobiological Laboratory of the Institute of Lake and River Fisheries. These observations were summarized by Gvozdev and Volkov (1978) and others.

In MO, all the fishes were killed by polychlorpinen in 1963. Later in 1975-1980 and in 1984, the lake was used for yearly rearing of fingerlings and yearlings of whitefishes (*Coregonus peled, C.nasus, C. muksun , C.lavaretus* and their hybrids) and also several other fishes. During the period of exploitation, the lake was fertilized with mineral nutrients and limed. In 1985-1987, the lake was not stocked with fish. However, the control fishing showed the presence of small amount of whitefishes which had apparently penetrated the lake from BO. A small number of *Carassius auratus* also remained in the lake from previous stockings. In 1988, larvae of peled and carp fry were released into MO (Table 1). As a result of low quality of the stocking material, the survival rate of peled larvae was very low (5%). Thus, in 1988, the fishes were represented in MO almost entirely by carps (212 kg per ha at the end of the season, Table 1).

BO, also devoid of native fish populations in 1963, was used for cultivating the youth of whitefishes and carp in 1971-1974, 1976, 1977, and 1981-1988. A detailed analysis of the results of fish rearing in BO was given by Tereshenkov et al. (1987) and Rudenko et al. (1989). This lake was also fertilized and limed in 1974-1984. During the period of investigations, the biomass of whitefishes at the end of the season was 85-138 kg per ha while that of carps — 140-230 kg per ha (Table 1).

Seasonal changes in total biomass of fishes in BO and MO were similar throughout all these years. Fig. 1 shows a typical example of biomass growth curve during 1986 for BO. The curve is S-shaped and reaches its maximum in late August-September. During the most part of the season, the diet of whitefishes included mainly zooplankton while that of the carp included

zoobenthos and detritus (Baranova and Yakovlev 1989).

3. Material and methods

3.1. Zoobenthos

In May 1986, samples of benthos were collected at 14 stations in BO and at 5 stations in MO. Later the number of stations similar in bottom deposits and faunal composition was reduced, and a few characteristic sites were chosen for the further study of macrobenthos. In BO, the samples were taken in the coastal area (at the depth of 1.5-1.8 m in brown mud with peat and macrophytes *Numphar lutea*, at the depth of 2.0-2.3 m on muddy sand) and in the deep part at the depth of 3.1 m. In MO, the samples were taken at the depth of 0.5-0.7 m on muddy sand with detritus, and at a depth of 2.2 m in the central part of the lake. In 1987-1988, the observations were carried out also at an offshore station at the depth of 0.7 m on muddy sand with detritus. Samples were taken two times a month in spring and in summer and once a month in autumn using the Petersen bottom grab with sampled area of $1/40$ m^2 or the tube bottom sampler with sampled area of $1/250$ m^2.

The results of analysis of the zoobenthos quantitative composition in BO were averaged for the lake with regard to the bottom area occupied by various biotopes.

3.2. Planktonic crustaceans and Chaoborus *larvae*

Zooplankton was sampled in both lakes from May to September-October. Sampling interval varied from 2 to 15 days depending on the water temperature (and, therefore, on duration of the cladoceran egg development). Except 1986, when samples were taken approximately every ten days, the sampling was more frequent in June to August than in May or September to October.

Zooplankton was sampled routinely with a modified eight litre Schindler-Patalas trap equipped with 120 μm plankton net at one (in 1986) or three (in 1986-1987) stations randomly distributed within the central part of the lake. At each station, eight-litre samples taken from three depths (surface, 1-2 m, near bottom layer) were combined into one composite sample. Each composite sample thus contained zooplankton from 24 (in 1986) or 72 (in 1987-1988) litres of water. Samples were fixed in formalin, examined and measured in the Bogorov counting chamber under a stereomicroscope. The estimate of biomass (Balushkina and Winberg 1979, Dumont and Balvay 1979).

3.3. Rotifers

Counting and identification of rotifer species (except *Asplanchna*) were made every 3-15 days from sediment samples (see Material and methods: Phytoplankton). The abundance of *Asplanchna* was determined from mesozooplankton samples simultaneously with determination of that of crustaceans and *Chaoborus* larvae. The biomass was determined by rotifer individual weights which were calculated using equations of isometrical growth (Winberg and Lavrentyeva 1982).

3.4. Infusoria

In each lake, the samples were taken at one standard station in the centre of the lake using a 1-liter water-sample bottle. Samples were taken from depths of 0.5, 1.0, 1.5, and 2 metres, then mixed to obtain an integrated sample from each lake. Samples were delivered to the laboratory in thermoses and immediately examined under the microscope and counted in the Bogorov counting chamber. A relatively high density of Infusoria permitted estimation of most species abundance in 30 ml of nonfiltered water. Large and rare Infusoria species were counted in 200 ml of lake water after preliminary concentrating on membrane filters (pore size 3-5 μm). Sampling intervals varied being shorter in May and during August-September when abundant development of planktonic protozoans occurred. The biomass of infusorians was determined by measurement of individual mean size under a microscope; the animals assumed to be similar in shape to geometric figures.

3.5. Phytoplankton and chlorophyll-a concentration

Samples were taken from March to November at one station marked with a buoy in deepest part of each lake. During the summers 1986 and 1988, samples were collected every 10 days while they were collected every 5 days in summer 1987. In spring (April) and autumn (September-November), the samples were taken two to three times a month. Phytoplankton was sampled with a 1.5 litre Ruthner sampler at 0.5 m intervals from the surface to the near bottom layer. A subsample of 0.5 litre from each portion of mixed water was fixed in formalin for species identification and cell counting. The remaining part of the mixed water was used for determinations of chlorophyll concentration and primary produc-

days. Each sample was subsequently concentrated to 50-100 ml with a siphon. Species composition and algal abundance were determined using Nagott counting chamber (0.02 ml) under a microscope. Small organisms were counted in 25-40 randomly chosen fields while large cells were counted in the whole chamber. Each sample examination was repeated 5 times. Biomass assessment was based on the individual volume of algal cells and their number. Mean cell volumes were estimated for all the species by measurements of 30-70 specimens approximated as a simple geometric shape. The biomass was expressed as wet weight assuming that the density of algae equals 1.00.

3.6. Bacterioplankton

Total numbers of bacteria were determined on Synpor N 8 membrane filters with erythrosine staining (Razumov, 1932). Integral samples were collected each 5-30 days. Cocci of two size classes (mean diameters 0.4 and 1.6 μm) and bacilli (mean sizes 0.3×3.0 and 1.2×5.0 μm) were counted separately. In calculation of biomass, the correction coefficient (1.6) was used to account for change in the bacterium specific weight as a result of drying (Romanenko and Dobrynin 1978).

The degree of bacterioplankton aggregation was studied simultaneously with the estimation of bacterial production rate (Pavelyeva, unpublished data). ^{14}C hydrolysate of plant protein was added to water samples filtered through a nylon mesh (pore diameter 20 μm). Samples were exposed at natural temperature in an aquarium for 2 hours. After exposure the water was filtered through membrane filters Synpor with pore diameters of 2.5 or 0.2 μm. Every filter was washed with 20 ml of water, cleaned of suspension and dried. Radioactivity was determined with a scintillation counter. Aggregation (the portion of bacteria associated with detritus) was calculated in relation to the radioactivity of two fractions, assuming that a fraction < 2.5 μm includes separate bacterial cells and fraction 2.6-220 μm includes aggregates.

3.7. Assessment of relative abundance of organisms in the lakes

A relative abundance index was used for comparison of the BO and MO communities. This index was calculated as a logarithm of ratio between the abundance (numbers or biomass) of organisms of a particular taxon in BO and their abundance in MO. Positive values of the index indicate that these organisms were more numerous in BO than in MO, while negative values demonstrate that the abundance is lower in BO. Mean individual weights of animals, water transparency, and chlorophyll content were compared in the same way. The following values were used:

RB_C — relative biomass of planktonic crustaceans;

RW_C — relative mean individual weight of planktonic crustaceans;

RB_R — relative biomass of planktonic rotifers;

RB_I — relative biomass of planktonic ciliates;

RN_B — relative number of bacteria;

RB_P — relative biomass of phytoplankton;

RSD — relative Secchi depth;

RCH — relative chlorophyll-a content.

4. Results

4.1. Benthos

A total of 101 taxa of macrobenthic animals were found in BO. Chironomid larvae were the most diverse and numerically abundant group. Their biomass constituted 70-90 % of total biomass of macroinvertebrates in the lakes, though some individuals of Oligochaeta, Hirudinea, Ephemeroptera, Trichoptera, Heleidae, Hydracarina, Coleoptera, Planaria, Diptera, Hemiptera, Gastropoda, Bivalvia also occurred.

Maximum species diversity and biomass of benthic animals were observed in the littoral. In the liquid mud of each lake central part, only sparse populations existed presumably due to the low oxygen content in the near bottom layer of water (Golubkov, personal observation). Larvae of *Glyptotendipes paripes* Edwards were the dominant group in both lakes. Subdominant groups in BO and MO were the larvae of *Chironomus cingulatus* Meigen and *Endochironomus impar* (Walker), respectively.

The dynamics of biomass and numerical abundance of benthic animals in BO during ice-free seasons 1986-1988 is shown in Fig. 2. Arrows indicate the time of stocking of young carps in the lake. As it is seen from Fig. 2, the dynamics of certain values in these years was quite similar. In late spring — early summer, the biomass and numbers of individuals increased but later, in middle and late summer, these values abruptly decreased. A decline in the biomass and numbers of benthic animals was observed in mid-June 1986, in in the second half of July 1987, and in mid-August 1988. Percentage of predatory chironomid larvae in the total numbers of individuals of this group in BO varied slightly in 1986-1988 (Fig. 2).

Erpobdella octoculata L. and *Helobdella stagnalis* L. are active predators predominant among the seven leech species inhabiting the littoral zone of both lakes. *Haemopis sanquisuga* L. occurred much less frequently.

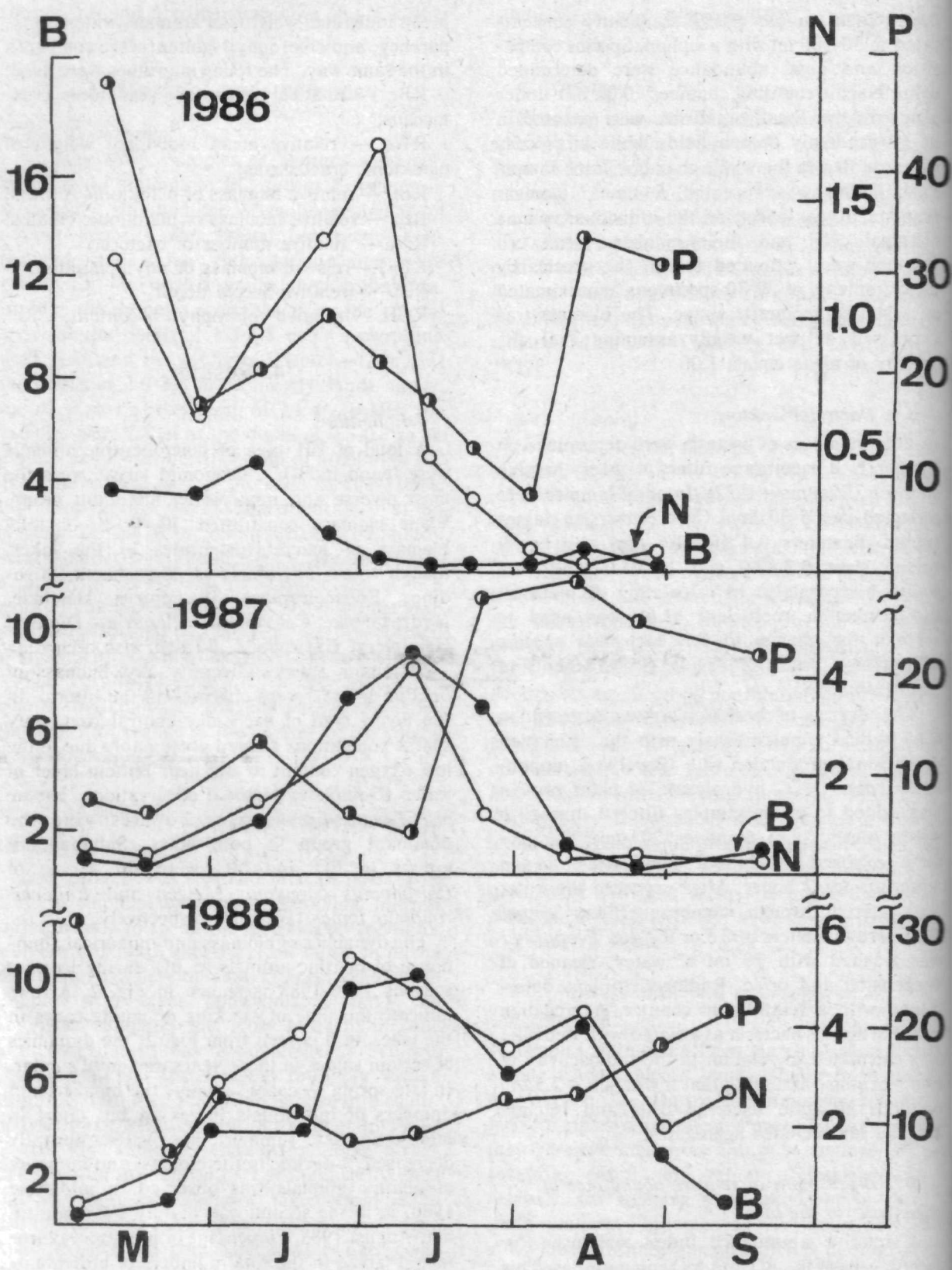

Fig. 2. Seasonal dynamics of macrobenthos numbers (N, 10^3 ind/m^2), biomass (B, g/m^2) and the percentage of predators in the total biomass of chironomid larvae (P, %) in BO during summers of 1986-1988.

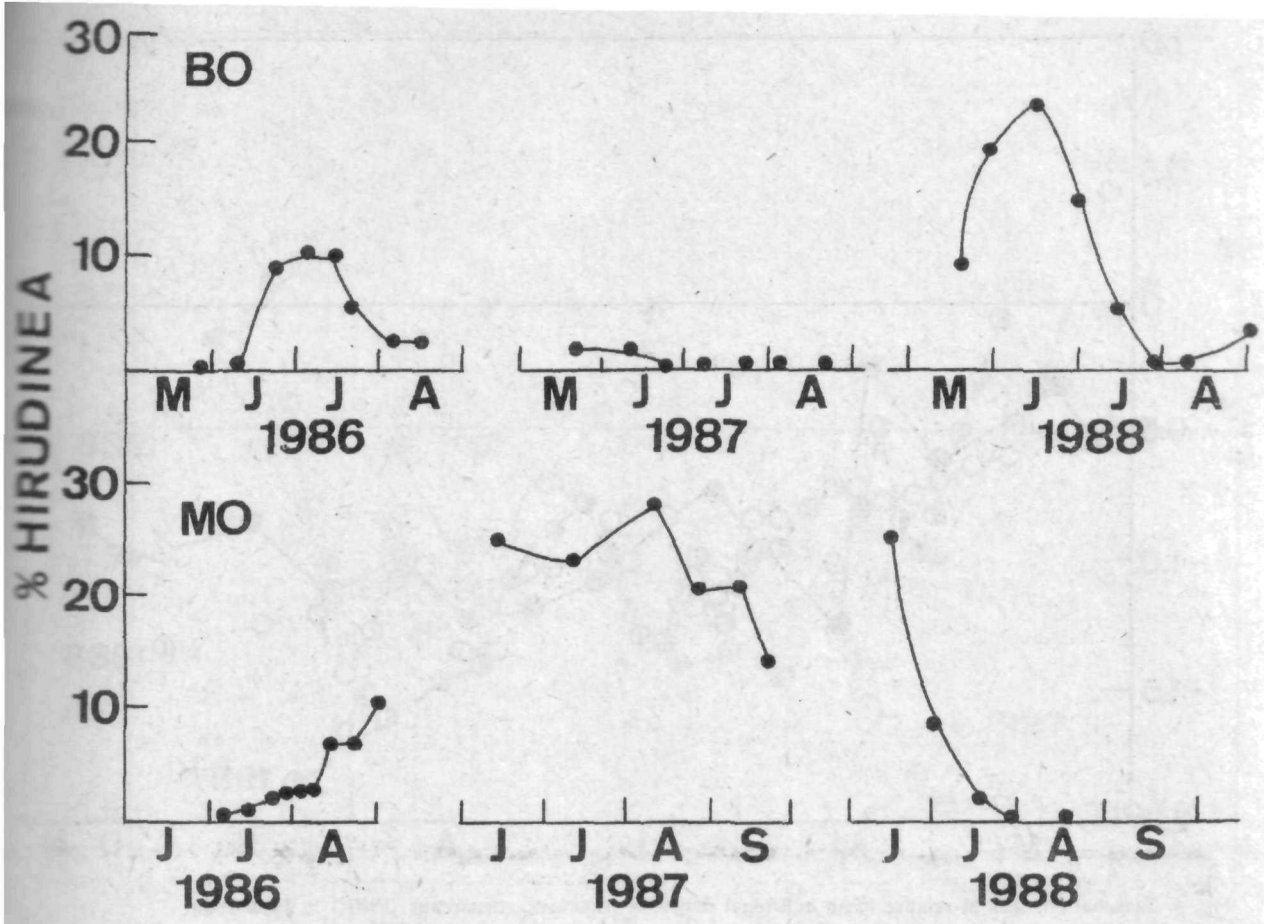

Fig. 3. Percentage of Hirudinea in the total biomass of macrobenthos in BO and MO (smoothed with the gliding average).

The percentage of leeches in the biomass varied during the season and in different years (Fig. 3) demonstrating a negative correlation with the fish density. In 1986, after stocking of BO with young carps, the portion of leeches began to decline and the leeches did not occur in the samples in late summer. The same trend was observed in 1987. In 1986 and 1987, the major part of leech populations inhabited areas near the coast living among roots of land plants, snags, and small plant remains. In 1988, when the mean abundance of young carps was notably lower than in previous years, the relative abundance of leeches in the total zoobenthos biomass of BO increased again (Fig. 3, a). Leeches occurred almost everywhere in the lake coastal zone.

In 1986, MO harboured a small number of large individuals of mirror carp which remained in the lake after stocking of the previous years. The percentage of leeches *H. stagnalis* and *E.octoculata* in total biomass was low (Fig. 3,b), and almost all individuals were found near the coast. In 1987, no fish was found in MO after the winter oxygen depression. Leech populations were quite abundant; their biomass in the lake littoral zone, free from macrophytes (st. 5), reached 28 % of the total zoobenthos biomass. Leeches were invariably present everywhere in coastal areas. In early summer of 1988, they constituted a large part of total biomass of benthic animals. However, after stoking of carps, *E. octoculata* completely disappeared from the bottom communities of open parts of coastal areas, and H. stagnalis was much less numerous than in the previous years. The relative abundance of leeches in the littoral zone free from macrophytes (st. 5) declined considerably (Fig. 3, b). They were present among coastal macrophytes throughout the whole ice-free season of 1988 (V.E.Panov, pers. comm.).

4.2. *Planktonic crustaceans and* Chaoborus *larvae*

Copepods dominated in plankton of BO from May to September (sometimes exeeding 90% of the total crustacean biomass). *Thermocyclops crassus* was the most numerous species among copepods (up to $7.08 \cdot 10^5$ individuals per m^3, 2.65 g/m^3). *Mesocyclops leuckarti* occurred in

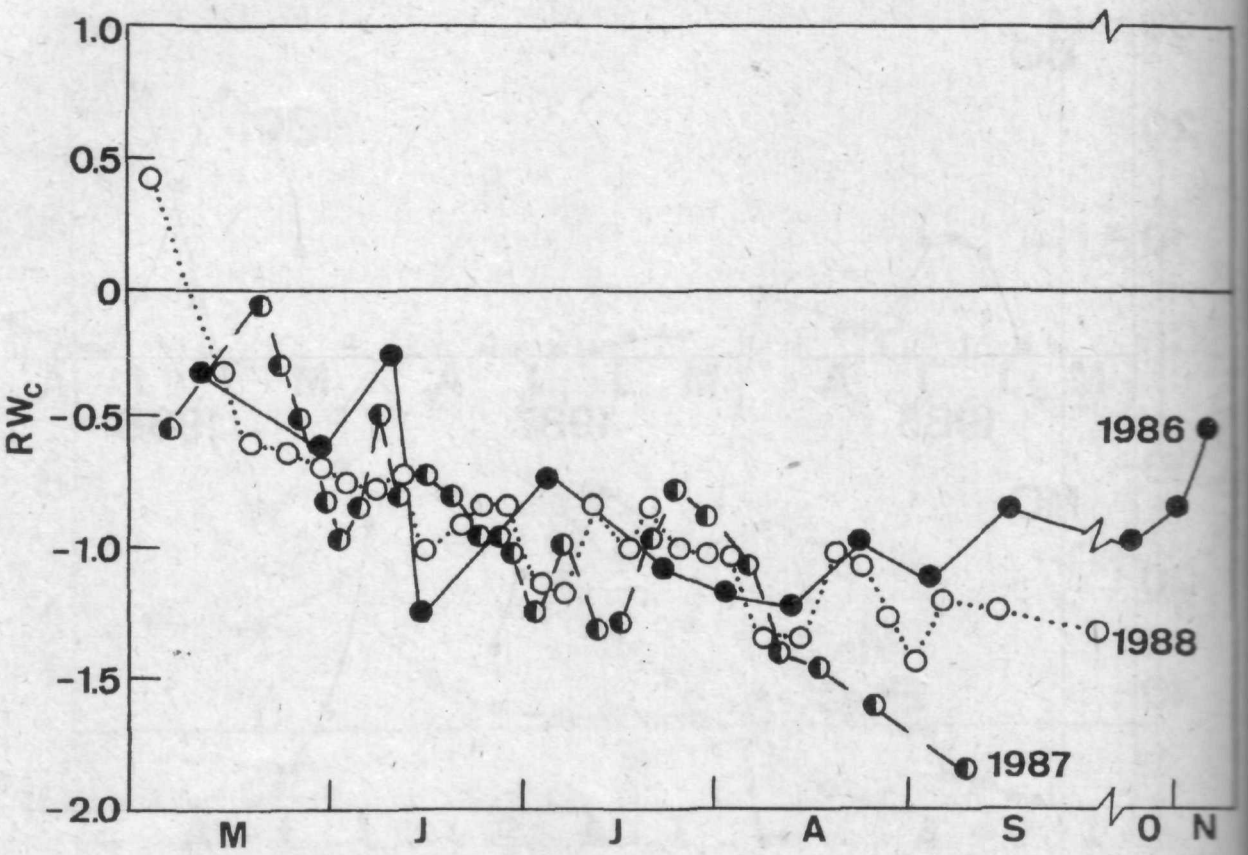

Fig. 4. Seasonal changes in relative mean individual weight of planktonic crustaceans (RW_C) in 1986-1988.

the plankton during the same period as *T.crassus*, being the second in abundance among copepods. In spring (May, early June) and autumn (late September-November), *Cyclops kolensis* prevailed among copepods. Diaptomids (*Eudiaptomus gracilis*) were present in plankton throughout the whole season of 1986 (about $1 \cdot 10^4$ ind/m^3) while only occasional specimens of *E. gracilis* were found in 1987-1988.

Bosmina longirostris (about $3 \cdot 10^3$ ind/m^3, 1.44 g/m^3) and *Daphnia galeata* (about $3 \cdot 10^4$ ind/m^3, 0.52 g/m^3) were most abundant among Cladocera in BO. The populations of other *Daphnia* species, namely *D.longispina* and *D.cucullata*, remained less numerous (up to $3 \cdot 10^2$ ind/m^3) during the whole period of observations. *Diaphanosoma brachyurum* and *Ceriodaphnia* sp. were rather rare. In November 1986 and June 1987, the abundance of *Chydorus sphaericus* increased up to $3.3 \cdot 10^4$ ind/m^3 or 0.16 g/m^3. *Leptodora kindti* occurred regularly in the plankton of BO reaching its maximum density ($1.1 \cdot 10^3$ ind/m^3) in the middle of summer. The maximum numbers of *Chaoborus flavicans* larvae (more than $3 \cdot 10^3$ ind/m^3) were observed in June

differed considerably from that of BO. Large *Daphnia longispina* (more than 90 % of total crustacean biomass) prevailed in zooplankton throughout the summer season. The larvae of *Chaoborus flavicans* were abundant (see Appendix 2). In spring and autumn, *Cyclops kolensis* played an important role in MO, but it disappeared from the plankton in summer. The numbers and biomasses of other crustaceans (*Bosmina longirostris, Mesocyclops leuckarti, Thermocyclops crassus*) were never high. The predatory cladoceran *Bythotrephes longimanus* was recorded only once in the whole period of investigations. Larvae and pupae of another large *Chaoborus* species, *Chaoborus obscuripes*, did not occur in standard quantitative samples; however, they were found in the net qualitative zooplankton tows and in the fish gut content (J.A. Dunaeva, personal communication).

The comparison of zooplankton dynamics in summer with values of planktivorous fish biomass in BO and MO allows to distinquish three groups of species (Table 2). The first group includes species (*Daphnia, Chaoborus*) which density declines as the fish predation pressure grows.

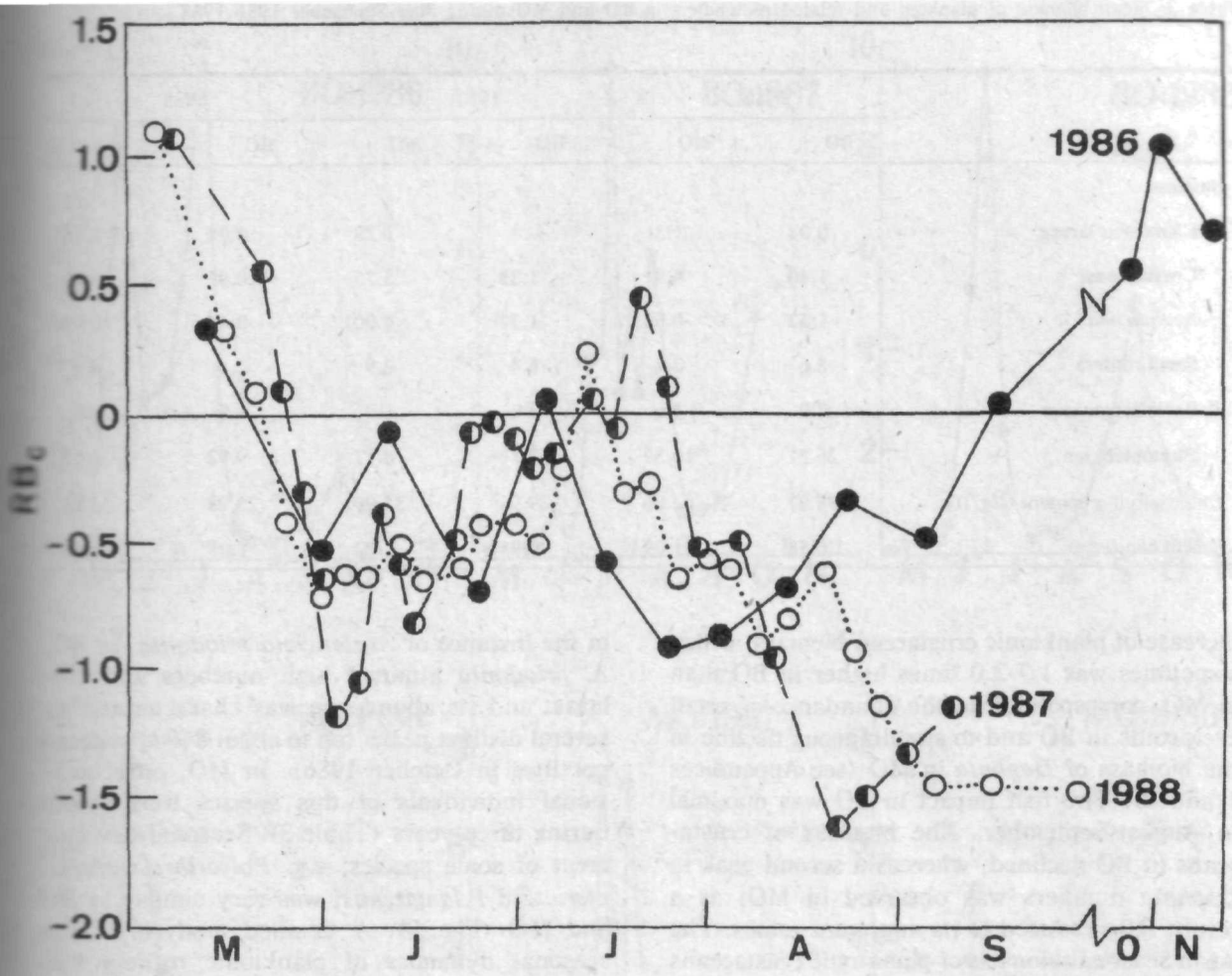

Fig. 5. Seasonal changes in relative biomass of planktonic crustaceans (RB_C) in 1986-1988.

The third group includes only *Endiaptomus* which dynamics has no apparent relation to the fish abundance.

Changes in the mean individual weight corresponded to those in the species composition of planktonic crustacean complex. The mean individual weight in BO was lower than that in MO throughout all the three seasons (Fig. 4). As fish impact increased during the season (Fig. 1), the difference between mean individual weights of crustaceans in BO and MO also increased while RW_C decreased. In late autumn, RW_C slightly increased after removal of the main bulk of fishes from BO.

The pattern of seasonal changes in relative biomass of planktonic crustaceans (RB_C) was the same in 1986-1988 (Fig. 5). RB_C was positive in the first half of May, i.e. the planktonic crustacean biomass was higher in BO than in MO; this can been explained by selective fish predation in BO during that period. As fish began to feed on crustaceans, and the total feeding rate increased, RBc declined (late May-June), however, later, its value had additional maxima. This

Table 2. Mean summer densities (10^3 ind./l) of planktonic crustaceans and *Chaoborus* larvae under high (BO:B_f = 85-140 kg/ha) and low (MO:B_f = 0-15 kg/ha) fish pressure on zooplankton. "P" — present in low numbers.

Group	Taxa	High fish pressure	Low fish pressure
I	*Daphnia*	4.52-14.45	31.14-64.16
II	Small Cyclopoida (*Thermocyclops, Mesocyclops*)	66.76-161.53	2.20-9.47
	Bosmina	5.31-81.21	P-0.06
	Chydorus	0.05-3.34	P
III	*Eudiaptomus*	0.01-3.58	0.15-1.15

Table 3. Mean biomass of plankton and related parameters in BO and MO during May-September 1986-1988.

	1986		1987		1988	
	BO	MO	BO	MO	BO	MO
Biomass						
Chaoborus larvae	0.02	1.31	—	1.29	0.08	1.49
Crustaceans	1.40	4.91	1.33	3.75	0.97	3.66
Asplanchna	1.52	0.061	1.77	0.001	0.42	0.003
Small rotifers	3.6	3.2	6.4	3.9	2.4	4.9
Bacterioplankton	2.9	1.6	3.0	1.0	1.5	0.9
Phytoplankton	26.71	16.39	12.71	8.17	9.92	9.17
Chlorophyll-a content ($\mu g/l$)	98.07	62.06	39.95	35.99	23.98	73.82
Secchi depth (m)	0.58	1.09	0.96	1.22	1.08	0.72

increase of planktonic crustacean biomass, which sometimes was 1.7-3.0 times higher in BO than in MO, corresponded to the abundance of small cyclopoids in BO and to simultaneous decline in the biomass of *Daphnia* in MO (see Appendices 1 and 2). The fish impact in BO was maximal in August-September. The biomass of crustaceans in BO declined, whereas a second peak in *Daphnia* numbers was observed in MO; as a result, RB_C reduced to its minimum values. The mean seasonal biomass of planktonic crustaceans was 0.97-1.4 mg/l in BO, and 3.66-4.91 mg/l in MO (Table 3).

4.3. Planktonic Rotifers

A total of 32 species of planktonic rotifers were found in the lakes during the period of study. Most of them belong to widespread forms characteristic of small lakes and ponds of temperate zone. Such species as *Keratella cochlearis* Gosse, *K.quadrata* Muller, *Polyarthra dolichoptera* Idelson, *P.longiremis* Carlin, *Filinia longiseta* Ehrenberg and *Asplanchna priodonta* Gosse were numerous in both lakes. *Trichocerca* (s.str) *elongata* Gosse, *Gastropus stylifer* Imhoff, *Ascomorpha ecaudis* Perty, *Lecane ludwigi* Eckstein, *Brachionus diversicornis* Daday, *Keratella irregularis* Laut were found only in BO; *Hexarthra mira* Hudson — only in MO. Abundance of these rotifers, except *K. irregularis*, was low.

Keratella cochlearis prevailed among the dominant rotifer species in both lakes, only in 1988 it was replaced by *K. irregularis*. The pattern of seasonal development of rotifers was different in MO and BO (Fig. 6): a second autumn peak of abundance occurred in BO which was never observed in MO. Significant difference in the instance of *Asplanchna priodonta*. In BO, *A. priodonta* attained high numbers and biomass, and its abundance was characterized by several distinct peaks (up to about 840 specimens per litre in October 1986). In MO, only occasional individuals of this species were found during three years (Table 3). Seasonal development of some species, e.g. *Polyarthra dolichoptera* and *P.longiremis*, was very similar in BO and MO (Fig. 7). A detailed analysis of the seasonal dynamics of planktonic rotifers was given by Telesh (1990, 1991).

In summer seasons of 1986 and 1987, the mean monthly values of biomass of small rotifers were constantly higher in BO than in MO. An opposite tendency was observed in 1988: the rotifer biomass was higher in MO during June-August (Fig. 8, Appendix 3). This reflected in the mean seasonal values of biomass: the mean biomass in BO in 1986 and in 1987 was higher and in 1988 lower than in MO (Table 3).

4.4. Planktonic ciliates

Among 36 species of planktonic ciliates occurred in BO (Appendix 4), *Strobilidium velox, Coleps hirtus, Stentor roeseli*, and *Stokesia vernalis* were dominant during 1986-1988. These four species were present in the plankton almost throughout the entire period of study, with peaks in spring and autumn. Ephemeral species, such as *Phaseolodon vorticella*, were abundant only during short periods.

In spring, ciliates achieved their greatest abundance. The maximum value of total numbers of Infusoria in the plankton of BO (recorded on 22 May 1987) was $5 \cdot 10^4$ ind/l (3.5 mg/l). *Strobillidium velox* was the most important spe-

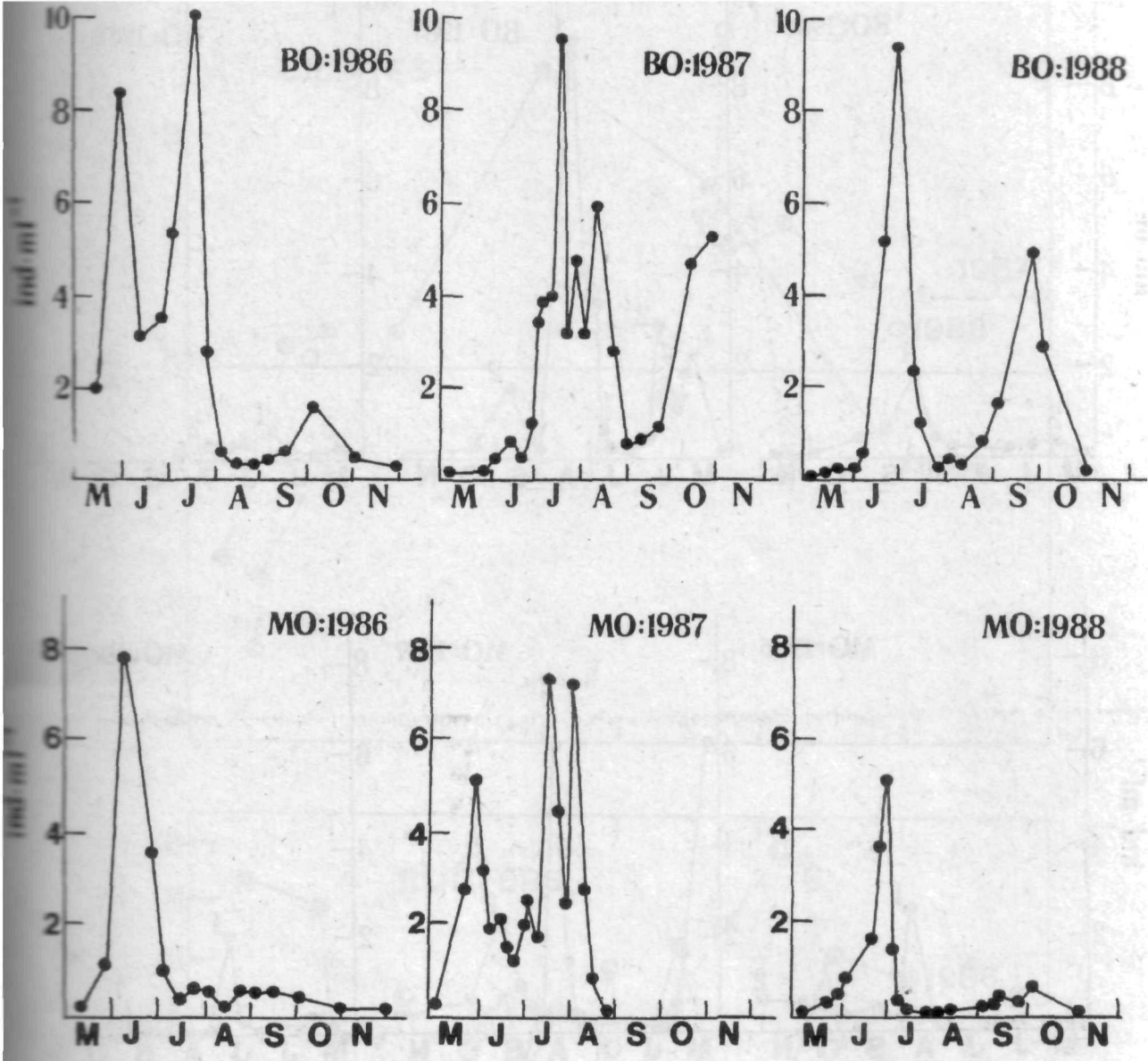

Fig. 6. Seasonal population dynamics of *Keratella* spp. in BO (upper panels) and MO (lower panels).

while *Coleps hirtus* had the highest numbers ($4.0 \cdot 10^4$ ind/l, 1.3 mg/l). In that period, the biomass of Infusoria in BO attained 46% of the total zooplankton biomass, 90% of phytoplankton biomass and 60% of bacterium biomass. Ciliates reached their spring peak of abundance earlier in 1988 (on 27 April) than in 1987; that peak was mainly connected with mass development of *Enchelys pupa* ($1 \cdot 10^4$ ind/l, 2.2 mg/l). In the middle of May, when coregonid larvae were introduced into the lake, ciliates were almost absent in the plankton. The autumnal increase of Infusoria abundance in BO was usually connected with mass species development (*Stokesia*, *Stentor*, and *Strobilidium*). In 1987, the autumn peak was observed in late October when the total biomass of Infusoria reached 2.7 mg/l; in that time, the biomass of *Stentor roeseli* was 1.4 mg/l (700 ind/l). In 1988, the autumnal peak of biomass was recorded earlier (19 August — 5 September); the biomass maximum values were 3.0-4.7 mg/l. Ciliates comprised up to 24-44% of the total biomass of zooplankton in that period; *Stentor* played the main role in the ciliate community (up to $2 \cdot 10^3$ ind/l, 4 mg/l). In August 1986, the mass development of *Coleps hirtus* was observed (about $3.6 \cdot 10^4$ ind/l) which coincided in time with mass mortality of *Microcystis aeruginosa*.

A total of 37 species of planktonic ciliates were found in MO (Appendix 4). Among them, *Bursella spumosa*, *Bursaridium* sp., *Tintinnidium*

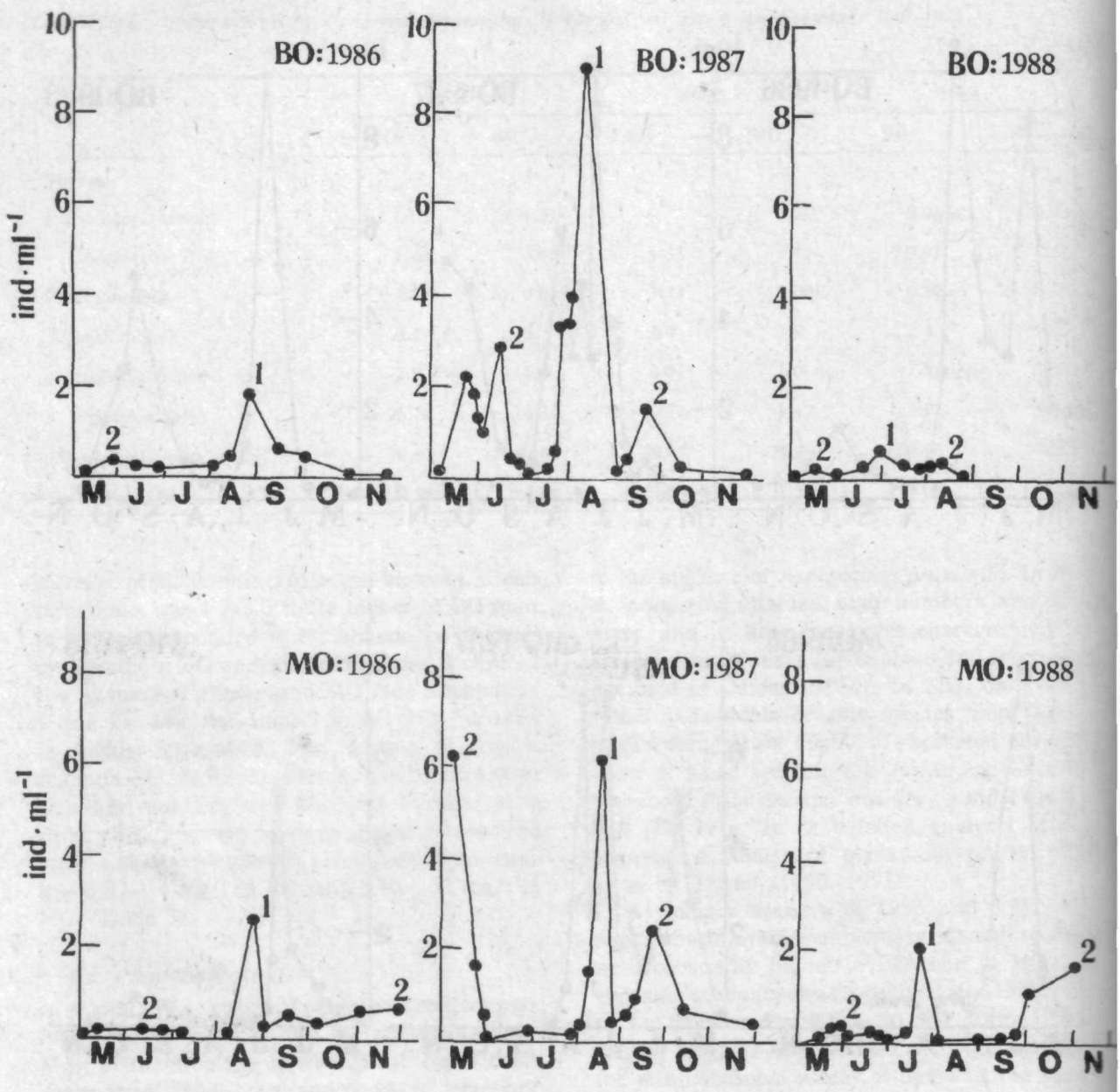

Fig. 7.Seasonal population dynamics of *Polyarthra* spp. in BO (upper panels) and MO (lower panels). Numbers indicate the dominant species: 1 — *P. dolichoptera*, 2 — *P. longiremis*.

fluviatile, *Strombidium mirabile* and *Prorodon ovum* were numerous during 1986-1988. There were no mass species of planktonic Infusoria common for BO and MO. Ephemeral species, characteristic of MO, included *Vorticella anabaena*, an epiphyte of cyanobacterium *Anabaena spiroides*. In 1988, a peak of abundance of *Loxodes rostrum* was observed. The spring maxima of planktonic ciliates in MO occured on 6 May 1987 ($1.1 \cdot 10^4$ ind/l: *Bursella, Tintinnidium, Bursaridium*); on 16 March 1988 ($1.28 \cdot 10^4$ ind/l: *Loxodes, Prorodon, Holophrya*); and on 27 April 1988 ($1.13 \cdot 10^4$ ind/l: *Prorodon, Bursella, Bursaridium*). In May 1988, the total ind/l; *Loxodes*, the abundant early spring form, almost completely disappeared from the plankton. Later, at the end of July, the numbers and biomass of cilates considerably increased, mostly due to large cells of *Loxodes rostrum* ($3.8 \cdot 10^4$ ind/l, 12 mg/l). In August, after the abundance of *Loxodes* decreased, the total biomass also decreased to 0.18 mg/l though in September it increased again (14.4 mg/l). Finally, relatively high numbers ($1.29 \cdot 10^4$ ind/l) and biomass (5.4 mg/l) of Infusoria were recorded under the ice in winter of 1988 (*Holophrya atra, Bursella spumosa, Loxodes rostrum, Spirostomum minus*).

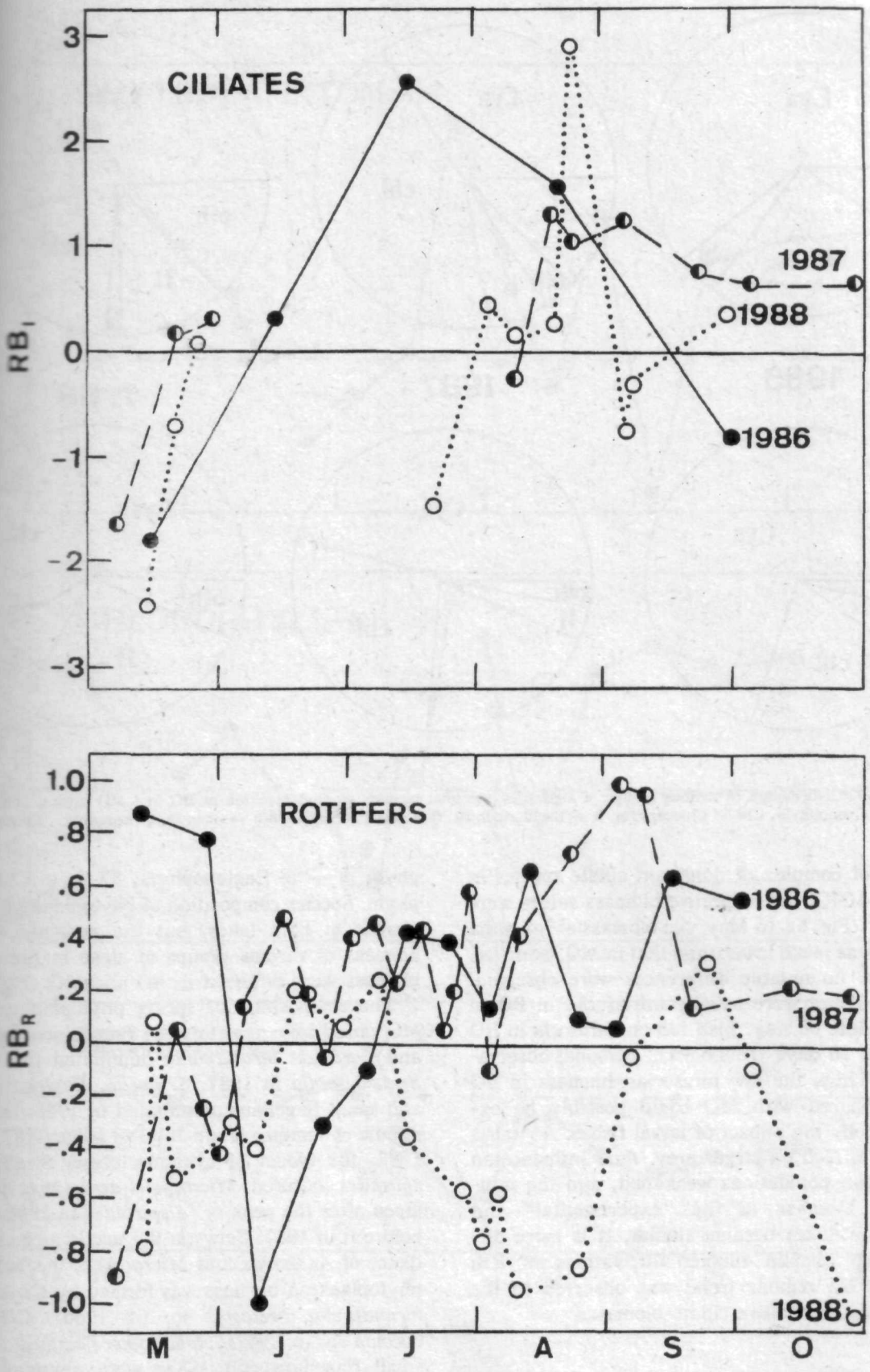

Fig. 8 Seasonal changes in relative biomass of planktonic ciliates (RB_I) and rotifers (RB_R) in 1986-1988.

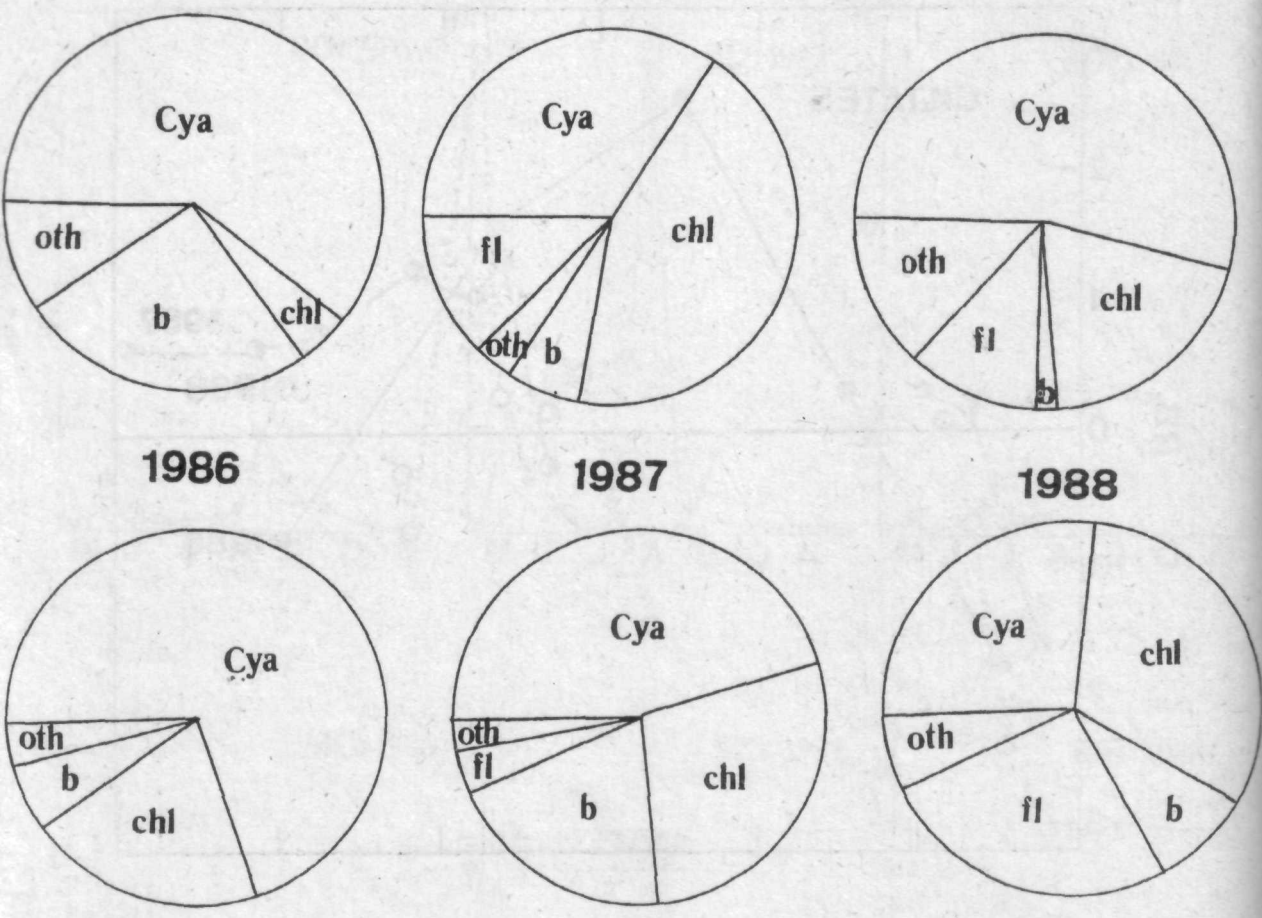

Fig. 9. Contribution of various groups of algae into the total biomass of phytoplankton in BO and MO during 1986-1988. Cya — Cyanophyta, Chl — Chlorophyta, b — Bacillariophyta, fl — small Flagellata, oth — other taxa (including Pyrrophyta).

sition of complex of dominant ciliate species in BO and MO, the respective biomass values were similar (Fig. 8). In May, the biomass of Infusoria in BO was much lower than that in MO, however, in June no notable differences were observed. Larval fishes were usually introduced in BO in the middle of May. Fish fed on Infusoria in BO for 7 to 10 days (Khlebovich, personal observation). Thus, the low infusorian biomass in BO as compared with MO could possibly be explained by the impact of larval fishes. As fishes began to feed on larger prey, their influence on protozoan populations weakened, and the infusorian biomass in the "experimental" and "control" lakes became similar. It is more difficult to explain further fluctuations of RB_I values. No regular trend was observed in the dynamics of relative ciliate biomass.

4.5. Phytoplankton and chlorophyll content

A total of 161 taxa were recorded from phytoplankton of two lakes. 29 of them belong to Cyanophyta, 3 — to Pyrrophyta, 3 — to Chrysophyta, 30 — to Bacillariophyta, 1 — to Xanthophyta, 8 — to Euglenophyta, 87 — to Chlorophyta. Species composition of phytoplankton was similar in both lakes, but the percentages of biomass of various groups of algae in the total biomass were different in BO and MO (Fig. 9).

The composition of spring phytoplankton in MO varied from year to year: *Trachelomonas* sp. and *Ceratium hirundinella* dominated in 1986, *Synura uvella* in 1987, *S. uvella, Euglena acus* and small flagellates dominated in 1988. In the middle of summer (June-July) of 1986, 1987 and 1988, the bloom of cyanobacterium *Anabaena spiroides* occured. *Microcystis aeruginosa* developed after the peak of *A.spiroides* in 1986 and before it in 1987. Between the maxima of abundance of *Anabaena* and *Microcystis*, the bulk of phytoplankton biomass was formed by *Ceratium hirundinella. Melosira* sp. (in 1986), *Chlorococcum* sp. (in 1987), *Aphanothece clathrata* and small flagellates (in 1988) were abundant in phytoplankton during the autumn.

In BO, the bloom of *Anabaena scheremetievi* was recorded in the middle of May of 1986 (up to 95 mg/l). In 1987 and 1988, the bloom was not observed in spring; chlorococcales *Dictyo-*

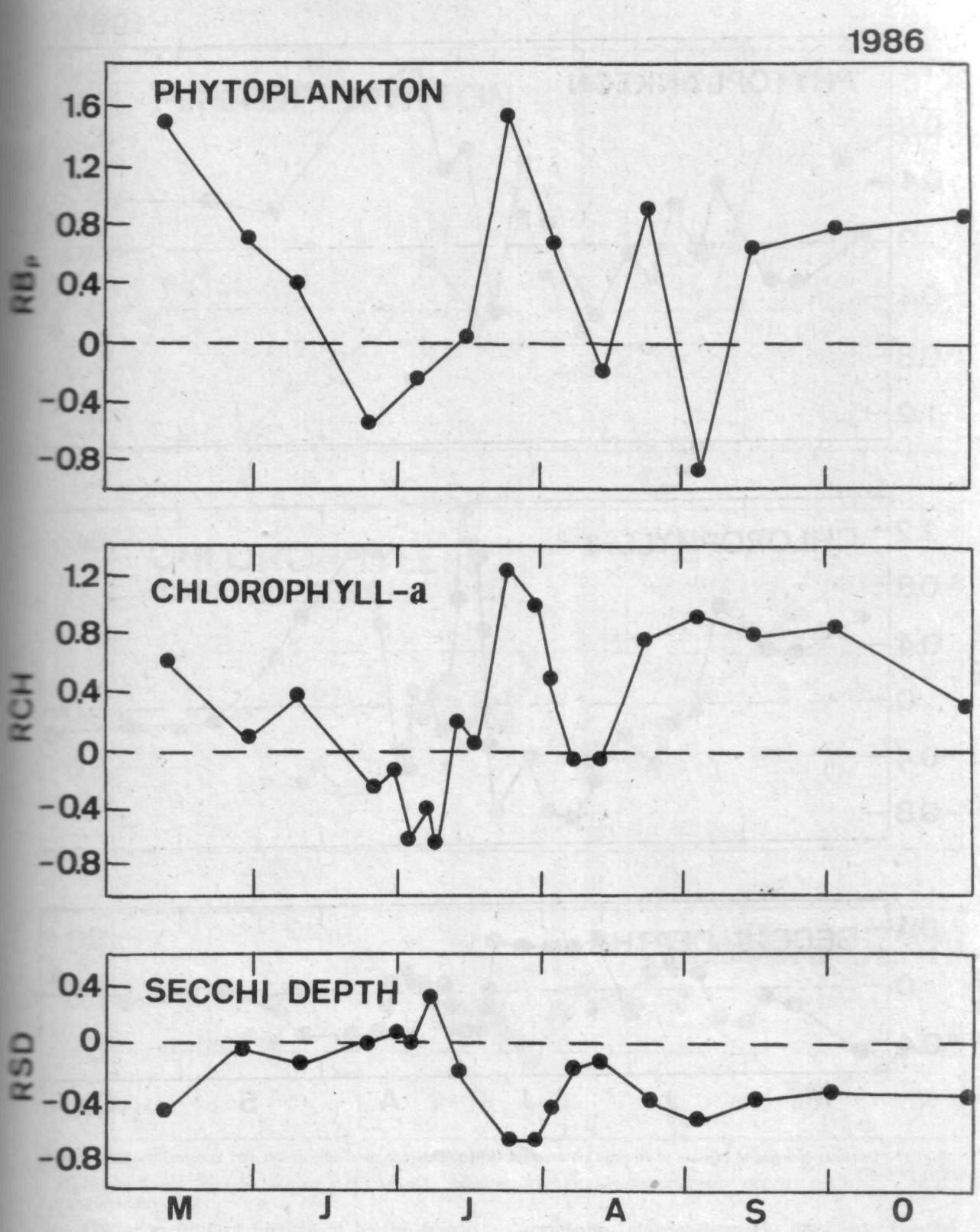

Fig. 10. Seasonal changes in relative phytoplankton biomass (RBP), clorophyll-a content (RCH) and relative Secchi depth (RSD) in 1986.

sphaerium pulchellum, *Chlorococcum* sp., *Scenedesmus quadricauda* and small flagellates were dominant in phytoplankton. During the summer, cyanobacteria *Gomphosphaeria lacustris, Microcystis pulverea*, and *Woronichinia naegeliana* were dominant in 1986, and *Aphanothece clathrata, M.pulverea, M.aeruginisa* and *A.clathrata* in 1987. Autumn phytoplankton was characterized mainly by diatoms, namely *Asterionella formosa*, species of the genera *Melosira* and

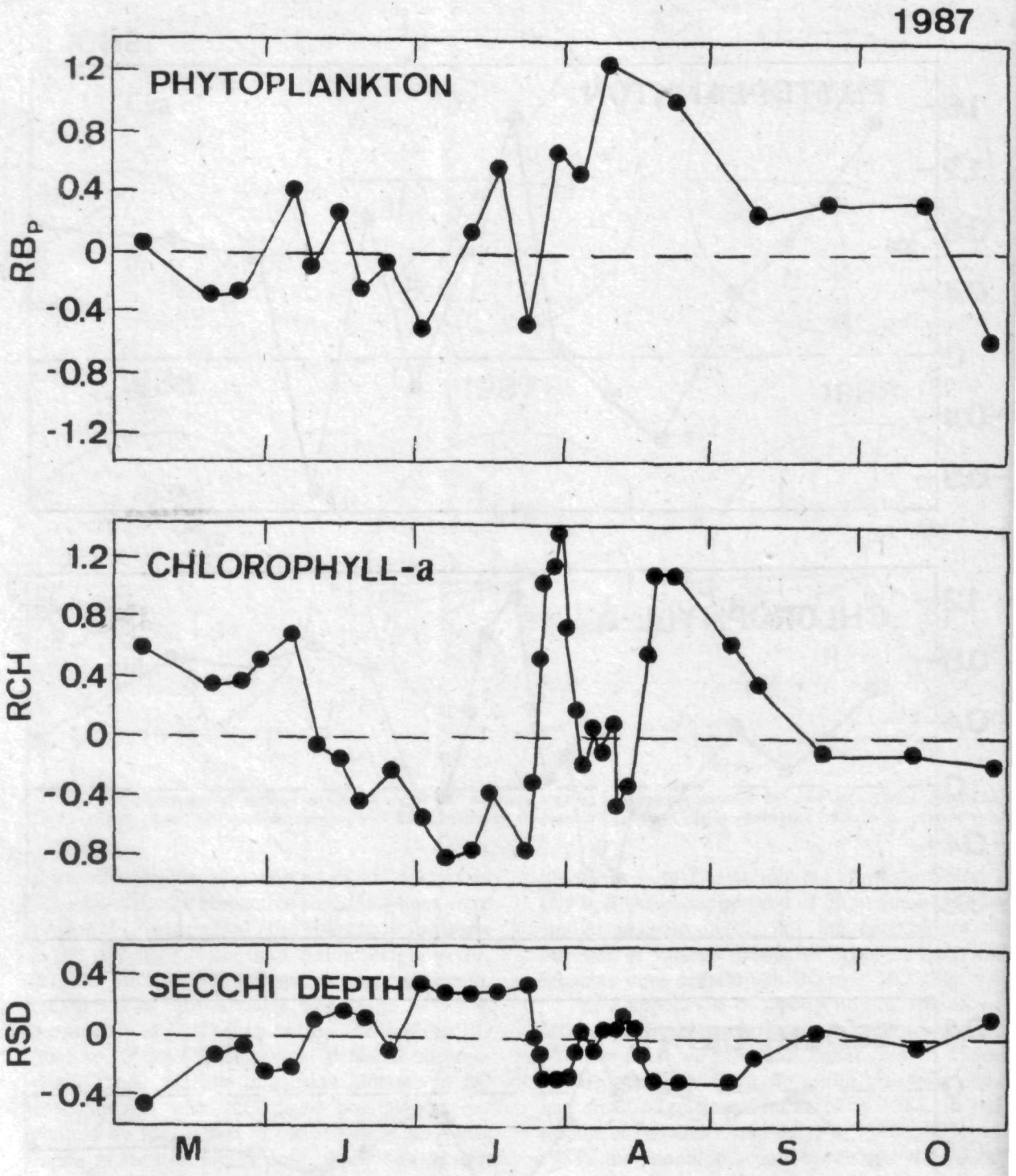

Fig. 11. Seasonal changes in relative phytoplankton biomass (RBP), chlorophyll-a content (RCH), and relative Secchi depth (RSD) in 1987.

Synedra. In 1986, cyanobacterium *Anabaena scheremetievi* was also abundant in autumn.

The mean monthly biomass of phytoplankton in BO varied during the season from 4.6 to 48.6 mg/l, that in MO — from 1.7 to 30.8 mg/l. Mean monthly chlorophyll-a content during the season was 7.0-144.1 μg/l in BO and 12.8-141.1 μg/l in MO. The mean water transparency (Secchi depth) varied from 0.49 to 1.50 m in BO and from 0.38 to 1.45 m in MO (Appendix 5).

Maximum differences between the lakes were observed in 1986 when the mean seasonal phytoplankton biomass and chlorophyll-a content in BO were 1.6 times higher and water transparency 1.9 times lower than those in MO (Table 3). Similar but smaller differences between the lakes

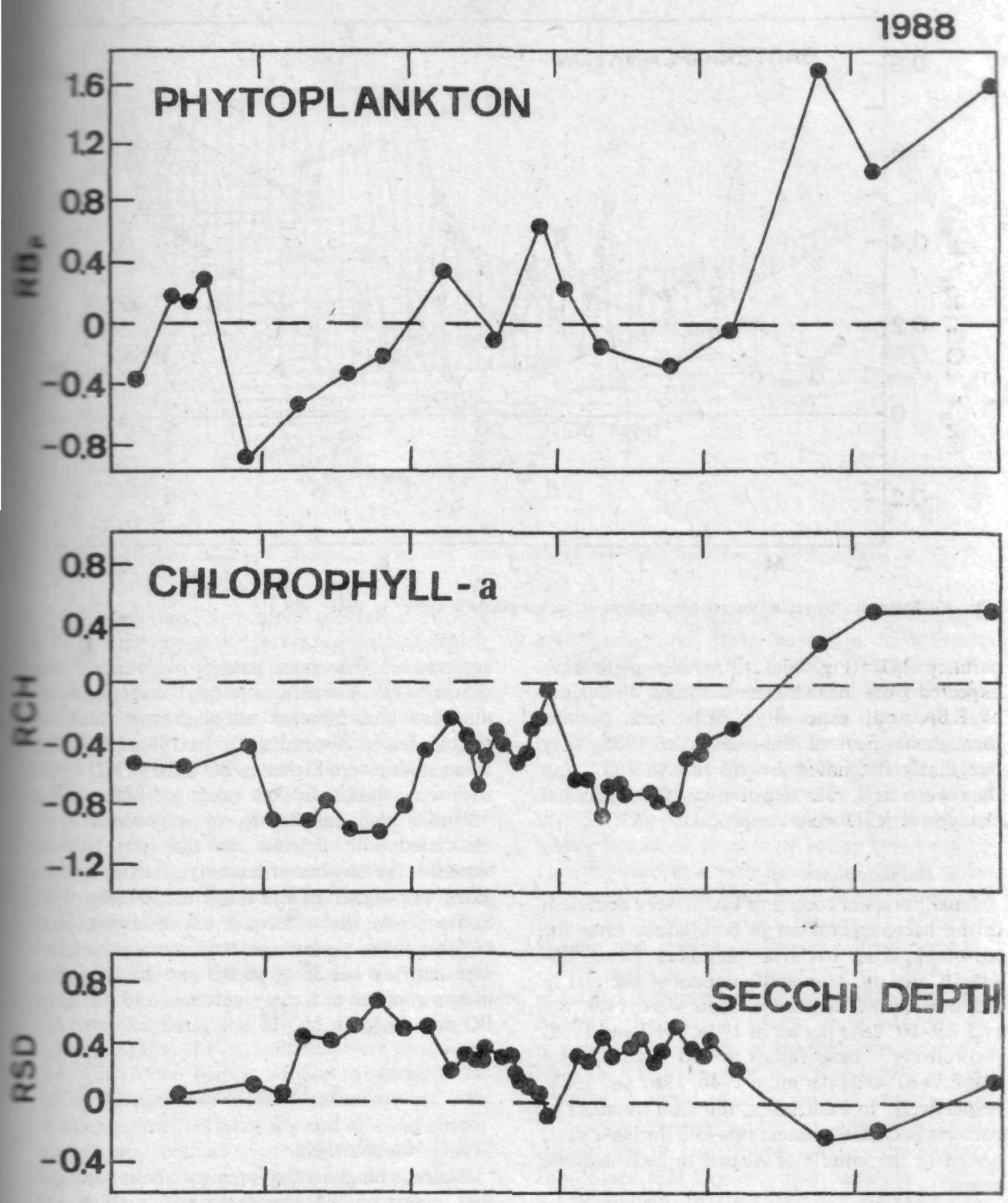

Fig. 12. Seasonal changes in relative phytoplankton biomass (RBP), chlorophyll-a content (RCH), and relative Secchi depth (RSD) in 1988.

were also observed in 1987. The phytoplankton biomass in BO was 1.5 times, and chlorophyll-a content was 1.1 times higher than those in MO. Accordingly, the water transparency was 1.3 times lower in BO than in MO. In 1988, the average seasonal values of phytoplankton biomass were very similar in the lakes, but the mean chlorophyll-a content was 3.1 times higher in MO than in BO, and water transparency was 1.5 times lower than in BO (Table 3).

Seasonal variations of relative biomass of phytoplankton (RBP) and of chlorophyll-a content (RCH) were similar and were negatively correlated with changes in relative water trans-

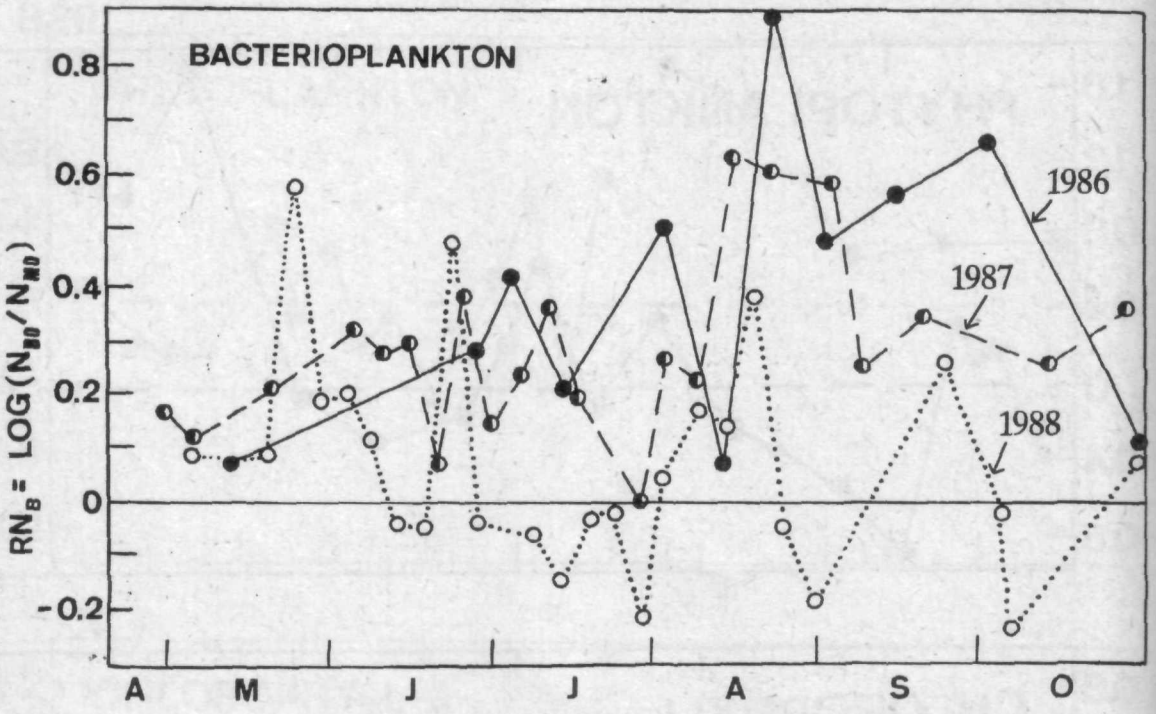

Fig. 13. Seasonal changes in the relative numbers of bacterioplankton (RNb) in 1986-1988.

parency RSD (Fig. 10-12). As one might have expected from mean seasonal values, the values of RB_P and, especially, RCh were positive throughout most of the season of 1986, they irregularly fluctuated around zero in 1987, and they were as a rule negative in 1988. Seasonal changes of RSD were reciprocal.

4.6. Bacterioplankton

Small forms of cocci and bacilli were dominant in the bacterioplankton of both lakes. After the ice-break, the bacterial numbers were 2.5-$4.0 \cdot 10^6$ per ml. Maximal numbers of bacteria in BO during the summer season were 14.9, 8.5 and $7.9 \cdot 10^6$ cells per ml in 1986, 1987 and 1988, respectively. These values in MO were 7.8, 4.4 and $8.9 \cdot 10^6$ cells per ml in 1986, 1987 and 1988, respectively. In both lakes, the total numbers of bacteria decreased almost two-fold during a short period in the middle of August in each of three years.

The complicated character of seasonal dynamics of bacteria in the plankton of two lakes hampers their direct comparison. However, the dynamics of bacterium relative numbers (Fig. 13) shows distinct differences in different years. In 1986 and 1987, when there were no fishes in MO, the bacterial abundance was considerably higher in BO than in MO ($RN_b > 0$). In 1988, when benthivorous fishes (*Cyprinus carpio*) and, to a smaller extent, planktivorous fishes (*Coregonus* spp) were introduced into MO, the values of relative abundance fluctuated irregularly around zero. The same pattern was revealed by comparison of mean monthly and seasonal numbers and biomass of planktonic bacteria (Table 3 and Appendix 6). In 1986-1987, the mean values were higher in BO than in MO while they were similar in both lakes in 1988.

Under the ice, 70 % of microflora were associated with detritus. In the first half of summer, the number of bacterial detritus aggregates was higher in BO than in MO (Fig. 14). Subsequently the difference between two lakes increased; the percentage of bacteria associated with detritus was 35 % in BO and 20 % in MO in late summer and early autumn, and 55 % in BO and 20 % in MO in late autumn.

5. Discussion

5.1. Macrobenthos

There is no general agreement about potential fish impact on the structure and abundance of zoobenthic community. According to some authors, there are evidences of such influence (Hayne and Ball 1956, Kajak 1977, Richardson et al. 1990) but other authors (Allan 1983, Thorpe and Bergey 1981) did not reveal the strong impact of fishes on the zoobenthos abundance. This disagreement may be connected with both principal and technical reasons.

The fundamental difference between benthic and pelagial communities results from the fact that the former are characterized by much more

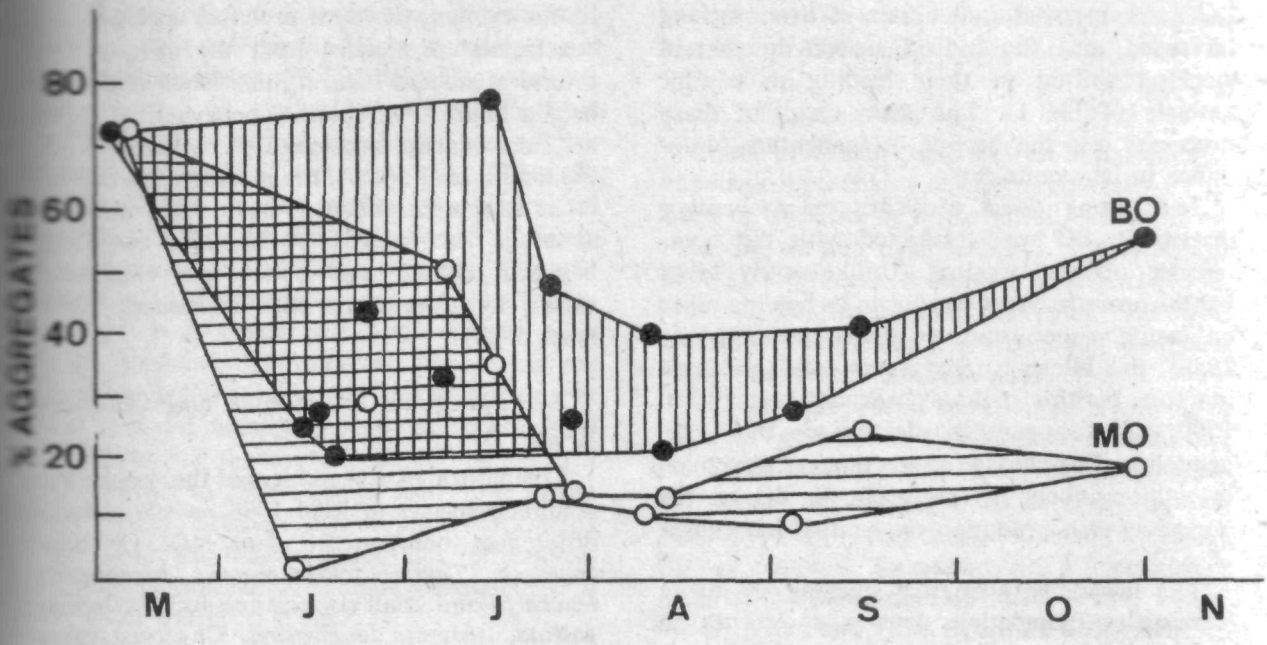

Fig. 14. Seasonal changes of percentage of bacterial cells associated with detrital particles in BO and MO.

complex habitats. Structured habitats provide a good refuge for invertebrate animals of which abundance and biomass thus cannot be controlled by fishes. This, in particular, accounts for weak fish impact on the zoobenthos dynamics in swiftly flowing rivers with stony bottom (Allan 1983). A similar situation may probably be observed on the stony littoral of lakes.

As to the technical problems, there is a vast body of available data which confirms the fish impact on pelagic animal communities obtained by the method of isolates. This method is much less applicable for benthic communities since many groups of benthic animals may use the walls of isolates as a substrate; this circumstance leads to distortion of experimental results (Thorpe and Bergey 1981).

In our study, the experiments were conducted in entire water bodies without disturbing the spatial integrity of bottom communities. The small experimental lakes BO and MO had simple unstructured bottom covered with mud. Macrophytes occupied only a small part of the littoral. This permitted assessment of fish impact in the absence of conditions where invertebrate animals could effectively avoid predators.

During the whole period of investigation, the consumption of benthic animals by fishes was the factor limiting the quantitative development of benthos in BO. This is consistent with the results of analysis of fish gut contents. According to the data of Baranova and Yakovlev (1989), after stocking of young carps in the lake BO (late May), planktonic animals were dominant in fish diet. With growth of fishes the planktonic animals were replaced by benthic ones. Carps of body mass over 10 g began to feed almost completely on benthic animals (if these were available in sufficient amounts). However, in late summer, the plant matter (namely detritus, mud, periphyton, macrophytes) became predominant in fish guts. Particularly high proportion of this food in the gut content (up to 85 %) was noted in 1986. The period when large amounts of plant matter appeared in guts of young carps approximately coincides with the period during which the benthic animal biomass in BO declined as a result of predation. This apparently allows to suggest that carps found another food sources.

The above-set data show that in 1986-1988, when fishes began to feed on zoobenthos, they become the major factor determining the numbers and biomass of benthic animals in BO. In 1986, when the stock of young fishes was the greatest, a rapid increase in fish consumption with their growth led to an almost complete elimination of zoobenthos in the beginning of July. Since that moment, fish began to feed on the other food. In 1987, the fish density in the lake was diminished almost two-fold as compared to 1986 (Table 1). Therefore, a similar situation in the benthic community was observed in a somewhat later period.

In 1988, owing to high mortality of young carps of first stocking (28th May) and their lower initial body mass (Table 1), the fish predation could not efficiently control the populations of benthic animals of which numbers and biomass rapidly increased (Fig. 2). In late summer, the predation by carps grew considerably because

the body mass of individuals of first stocking increased and the individuals of the second stocking shifted in their feeding to benthic animals (Table 1). The main result of these processes was the decline of zoobenthos abundance in late summer.

The strong effect of fishes on zoobenthos density in BO was connected with the peculiarities of carp feeding. Unlike many other benthivorous fishes, *Cyprinus* in its feeding relies on tactile rather than on visual cues (Sibbing 1988); this allows it to consume both active and inactive benthic animals (Richardson et al. 1990). This apparently determines the independence of percentage of predatory chironomids in total numbers of this group in BO on the impact of fish predation on benthic biocenoses (Fig. 2).

The low density of carp stocking led to an increase in population density of leeches in various biotopes of littoral zone. The high amount of leeches in biotopes free from macrophytes and other structured substrates is an unusual phenomenon. As a rule, leeches are associated with biotopes where a lot of macrophytes, stones, wood remains, etc. is present. Our data demonstrate, that in the case of absence or low density of fishes the leech populations may be abundant in habitats devoid of structured substrate. This may have been caused by more favourable feeding conditions in such zones. Efficiency of feeding in leeches declines abruptly with increase in density of plant substrates (Panov et al. 1988).

As the fish populations increase, leeches vanish from these zones. Thus, for instance, in the lake MO, when a large amount of young was stocked in 1988, leeches almost completely disappeared from the open part of the lake littoral but remained abundant among stems and leaves of *Numphar*.

At present, it is difficult to determine the specific mechanism for "exclusion" of leeches from the littoral without macrophytes by benthivorous fishes. There are published data showing that leeches may be eaten by fishes (Young and Spelling 1986; Spelling and Young 1987). However, leeches were not found in the stomachs of carps from the lakes BO and MO (Baranova and Yakovlev 1989).

Another possible mechanism of "exclusion" of leeches is the competition with fishes for food. Although not rejecting this mechanism completely, we should note that the biomass of chironomids, the essential food for *H. stagnalis* and *E. octoculata*, was sufficiently high in BO in 1987. Nevertheless, in 1987, leeches were extremely scarce in the open part of littoral (Fig. 3). In our opinion, the most probable mechanism of "exclusion" of leeches from the open part of littoral of studied lakes by the fishes could have been a kind of "territorial" behaviour of fishes, or, more exactly, avoidance of "collisions" with the fishes. In this case, the macrophytes like any other structured substrate could have served as a refuge for leeches. A negative correlation between leeches and fishes was established earlier in experiments with exclosures (Brönmark 1988).

5.2. *Planktonic crustaceans and* Chaoborus *larvae*

Comparison of assemblages of the zooplankton dominant species in 1986-1988 reveals essential differences between BO and MO. Cyclopoid copepods (*Thermocyclops crassus, Mesocyclops leuckarti*) and small cladoceran species (*Daphnia galeata, Bosmina longirostris, Chydorus sphaericus*) prevailed in the summer zooplankton of BO. In 1986-1988, relatively large *Daphnia longispina* and larvae of *Chaoborus flavicans* prevailed in MO. In 1989, when a large amount of whitefish fry was introduced in MO, the populations of *Daphnia* and *Chaoborus larvae* declined in June, and population of *Mesocyclops* raised later (P.I.Krylov, personal observation). As a result, the zooplankton community in MO became similar to that in BO. This observation suggests that fish impact was responsible for the observed differences in zooplankton composition between two lakes.

A decline in the populations of large planktonic animals (*Chaoborus, Daphnia*) and an increase in the numbers of relatively small species (*Thermocyclops, Mesocyclops, Bosmina, Chydorus*) under the fish pressure have been repeatedly observed (for reviews see Zaret 1980, Lazzaro 1987, Lyche 1989). It should be emphasized that the division of animals into 3 groups given in Table 2 cannot be considered as the general rule; it seems to be valuable only within a certain range of fish biomass. Thus, in communities where diaptomids prevail, an increase of fish predation results in an abrupt decline in the density of diaptomids (Beavers and Stavn 1975, Skoptsov and Krupennikova 1982). Sometimes an increase of fish predation may lead to complete elimination of planktonic crustaceans (Ziebell et al. 1986, Alekseev 1987). On the contrary, an appearance of small number of fishes in water bodies which previously contained no fish may lead to the disappearance of invertebrate predators feeding on preadult instars of crustaceans and, as a result, to the increase in populations of large herbivorous species as *Daphnia* (Archibald 1975, Northcote et al. 1978).

Whereas a decline in mean sizes of planktonic crustaceans under the fish pressure was suggested by many previous investigations, the fish influence on total zooplankton biomass is less obvious. According to a simplified scheme of trophic cascade (Carpenter et al. 1985), the growth of fish impact results in a decline of zooplankton biomass. On the other hand, selective elimination of large species may be compensated by mass development of small zooplankters; as a result, the total biomass may remain unchanged or increase (for review see Northcote 1988). Our study demonstrates that mean seasonal biomass of planktonic crustaceans was 2.8 to 3.7 times lower in BO (under fish impact) than in MO (without fish). Due to the mid-summer development of small cyclopoids which avoid the fish predation more effectively, the total crustacean biomasses were similar in both lakes during that time.

5.3. Planktonic rotifers

The numbers and biomass of small rotifers were sufficiently high in both lakes throughout the entire period of observations. An increase in the percentage of rotifers in zooplankton is characteristic of other small fertilized lakes of Syabero group (Potina 1985). An increase in the biomass of rotifers under high fish pressure similar to that recorded in BO (as compared with MO) in 1986 and 1987 was also observed in several other studies (Hrbacek 1962, Hurlbert et al. 1972, Lynch 1979, Dawidowicz and Pijanowska 1984, Bergquist et al. 1985). An increase in the biomass is usually accompanied by significant changes in the composition of assemblage of dominant species (e.g. Stenson 1982).

The mechanisms of these changes may be different. Besides the direct pressure of vertebrate and invertebrate predators as well as the interference with large filtrators, they also include changes in competitive relations in the plankton depending on the quality and quantity of algae and bacterial food. Complex of these causes has apparently led to a decline in the relative biomass of rotifers (RB_R) in July and August in 1988 as compared with 1986-1987 (Fig. 8).

An increase in the density of *Asplanchna* in zooplankton of BO obviously should not be considered as a result of fish introduction. It rather characterizes the general response of community to destabilizing factors, as was noted by Alekseev and Potina (1986) and Nekrasova (1988). An increase in the population of *Asplanchna* was also observed after removal of fishes from the lake (Stenson 1982). When one and the same factor operates for a long time, the planktonic community stabilizes, and the numbers and biomass of *Asplanchna* decline.

5.4. Planktonic ciliates

Ciliate protozoans may play an important role in pelagic food chains of lakes, especially in the lakes of high trophy (Stout 1980, Porter et al. 1985, Beaver and Crisman 1982, 1989). Nevertheless, with few exceptions (Stenson 1984, Miura 1990), this group of planktonic organisms usually was not taken into account in studies of "biomanipulation" and top-down effects.

The study of species composition of ciliates in different geographic regions has shown that similar habitats are often occupied by the same widespread species. The differences between geographically remote communities of freshwater ciliates manifest themselves in a quantitative ratio of the same species (Aliev 1989, Lokot' 1987). Therefore, the essential differences in species composition of ciliates between neighbouring BO and MO communicating by means of a channel are surprising.

During 1986-1988, both lakes had 21 common ciliate species out of 53 species found. The lakes had no abundant common species. In 1986-1989, *Stokesia vernalis* and *Coleps hirtus*, which were numerous in BO, did not occur in MO.

Several mechanisms of indirect fish impact on ciliate species composition and abundance may be assumed. Apparently, the relationships between protozoan and multicellular zooplankton, including competition for food and interference of rotifers and crustaceans (Stenson 1984, Gilbert 1989), may play an important role. During the period of investigations, the densities of *Daphnia longispina* and *Strobillidium* were negatively correlated. Qualitative and quantitative changes in the density of invertebrate predators (*Chaoborus* larvae, copepodites and adults of *Mesocyclops leuckarti* and *Thermocyclops crassus*, rotifers *Asplanchna*) capable of intensive feeding on protozoans (Krylov 1989) could also have been of importance. The planktonic community could be influenced to a certain extent by complicated relations between the major food sources of protozoans, i.e. bacteria and small phytoplankton (Stone 1990).

5.5. Phytoplankton and chlorophyll-a content

Several studies have revealed that the rearrangement of trophic chain after the change in fish density leads to considerable changes in the phytoplankton composition and abundance. The type of these changes varies and depends on several factors including trophy (McQueen et al. 1986). Whereas a decline in fish density and an increase in large cladocerans is occasionally

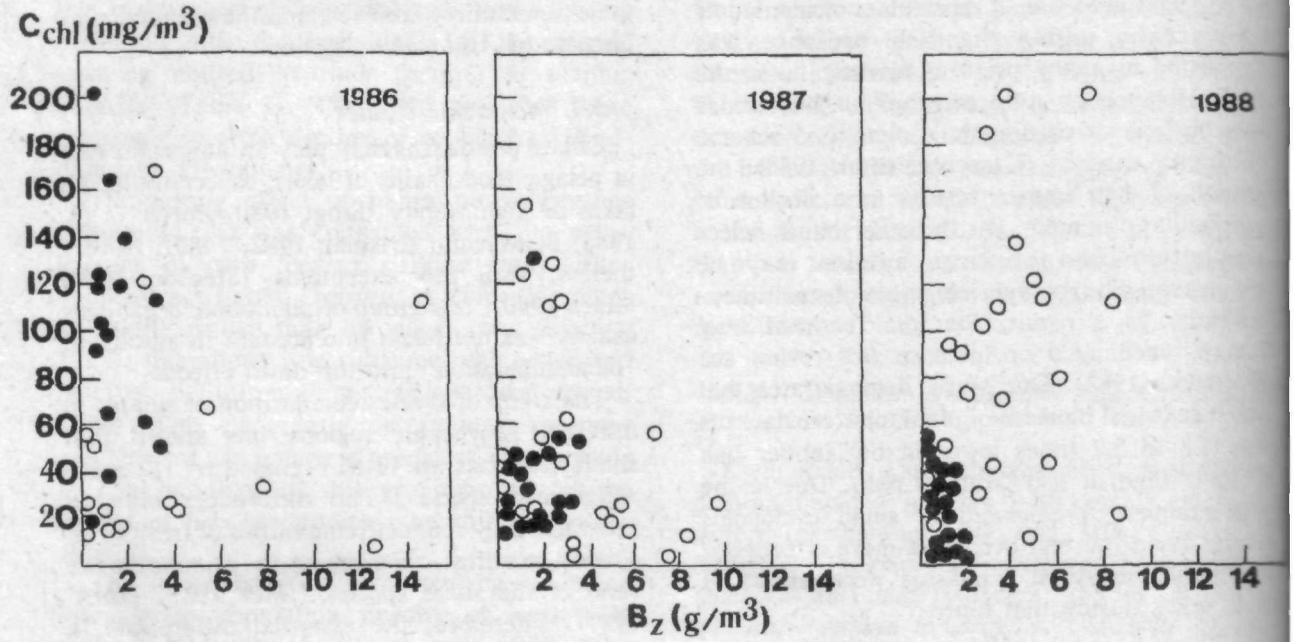

Fig. 15. Chlorophyll-a content (C_{Chl}) plotted against the zooplankton biomass (B_Z) in MO (open cirlces) during 1986-1988 summer seasons.

accompanied by a decline in the abundance of phytoplankton, in other cases the mass development of inedible forms of algae occurs (Lyche 1989). Thus, in many hypertrophic lakes, the summer development of large cladocerans coincides with the bloom of colonial forms of blue-green algae (Shapiro 1980, Lynch and Shapiro 1981).

Eutrophic lakes BO and MO well illustrate the latter example. In MO, where planktivorous fishes were absent and large *Daphnia longispina* dominated in zooplankton, the bloom of *Anabaena spiroides* was observed in the mid-summer. A decline of the biomass of phytoplankton and chlorophyll-a concentration in MO as compared with BO was observed in 1986-1987; however, it was not so pronounced as in some other biomanipulation experiments. The review of the whole lake experiments also indicates that, in water bodies of high trophy, the biomass of phytoplankton after reduction of fish abundance may decrease, remain unchanged or even increase (Lyche 1989).

The gap in the "zooplankton-phytoplankton" link of the trophic cascade observed in the present study is confirmed by the lack of close relation between the zooplankton biomass and chlorophyll-a concentration (Fig. 15). At high zooplankton biomass (more than 6 g/ m^3), both low and high (100-200 mg/m^3) concentrations of plant pigments were observed.

Although McQueen and co-authors (op. cit.) failed to find a relationship between the chlorophyll concentration and the total biomass of zooplankton, they noted a correlation between chlorophyll and the percentage of large efficient filtrators (*Daphnia*) in the zooplankton. In our case, such a relation would have meant that the chlorophyll concentration should be higher in MO (where the zooplankton was represented mainly by *Daphnia*) than in BO where copepodites of cyclopoids and small cladocerans dominated during the summer. This, however, was observed only during one of three seasons (in 1987, Fig. 15 b).

5.6. *Bacterioplankton*

Numbers of bacteria in 1986 and 1987 were higher in BO than in MO, in 1988 the respective values were more similar. Since in 1988 the benthivorous fishes affected the ecosystem of MO, one would think that the increase in bacterial numbers in MO was the result of high perturbation of bottom sediments by fishes, which in shallow lakes may increase the enrichment of water by nutrients and stimulate the development of some groups of bacteria (Lammens 1988, Tatrai et al. 1990 and references therein). A certain role in the increase of dissolved organic matter available for bacteria in the lakes may belong to the fish excretion (Antipchuk et al. 1977).

Microbiological studies of fishponds have revealed that the abundance and production of

bacteria are higher in more productive and more intensively used ponds (Antipchuk 1976, 1983, Kamlyuk et al. 1983, Voronova 1985). However, intensively exploited ponds usually receive more fertilizers and also may be enriched by remains of artificial food for fish. Therefore it is not possible to distinguish the effects of external nutrient additions from those of internal eutrophication related to fish activity (Opuszynski 1980).

Several studies of bacteria in natural waters and enclosures after experimental manipulation with fish density (Opuszynski 1980, Hessen and Nilssen 1986, Riemann and Sondergaard 1986, Tatrai et al. 1990) give some evidence of multiple causality responsible for an increase in bacterial numbers in the presence of fish. These causes are the direct input of dissolved organic matter with excretions into water, perturbation, and change in absolute and relative abundance of unicellular (Stone 1990) and multicellular (Vaque et al. 1989) zooplankton.

The percentage of bacteria associated with detrital particles was higher in BO than in MO. As it is known, protozoans (Albright et al. 1987) and small crustaceans (Bern 1990) can feed more intensively on single bacterial cells. As the body size of planktonic crustaceans increases, the role of single bacterial cells in their feeding decreases while that of larger particles increases (Schoenberg and Maccubbin 1985, Knoechel and Holtby 1986). Since small zooplankton was abundant in BO during all three years of observations, the zooplankton impact in this lake could be directed mostly to single bacterial cells. This probably determined their smaller portion in the total amount of planktonic bacteria.

5.7. General discussion

The main result of fish impact on ecosystems of investigated lakes was the change in the structure of food chains both in plankton and benthos. In both these communities, a decline of fish impact was accompanied by the development of populations of large invertebrate predators (larvae of *Chaoborus* in the plankton and leeches in the benthos) and alternative food chains associated with them.

It should be noted, however, that a decline in fish impact did not lead to the development of population of small invertebrate predators such as predatory chironomid larvae in benthos and/or cyclopoid copepods in plankton. There are grounds to believe that in this case one kind of "key predators" (fishes) was replaced by another one (*Chaoborus*, leeches) controlling the development of food chains. Therefore, the predator potential for playing a "key role" in the community may be inversely related to the predator mean size.

In planktonic communities, the dense stocking with planktivorous fish (the major "key predator") led to change in the entire structure of food relations: dominance of cyclopoids and an increase in the role of small zooplankton. In benthic communities, the variations of fish impact did not result in diverse rearrangements of food chains which was apparently related to non-selective (as compared with peled) burrowing feeding of carps. Stocking of carps in MO in 1988, besides the direct effect on zoobenthos, significantly affected the components of pelagic food chain.

The relative abundance of heterotrophic bacteria, concentration of chlorophyll-a, and rotifer biomass increased whereas the water transparency (Secchi disc depth) declined. Large ciliates *Loxodes rostrum* gave outbreaks which were not observed before. These data show that indirect influence of benthivorous fishes may play an important role in the regulation of structure and dynamics of a planktonic community in shallow lakes. Variations in fish impact result primarily in essential structural rearrangements of ecosystem but changes in the ecosystem structure inevitably lead to changes in its functioning. Further studies on structural and functional characteristics of ecosystems and a quantitative assessment of the relations between their components would provide valuable insight in the problem of "top-down" regulation.

Acknowledgements

We are grateful to B.L.Gutelmacher, K. Aarbaciauskas, and T.L. Lazareva for help in collecting and processing the zooplankton samples, to S.M. Glagolev, V.R.Alekseev and J.A.Dunaeva for identification of *Daphnia*, *Cyclops*, and *Chaoborus* larvae species, to G.P.Rudenko, A.S.Yakovlev, A.S.Pechnikov for the data on fish population dynamics, to T.L.Lazareva and V.G.Vlasova for drawing figures and technical assistance during the manuscript preparation.

References

Albright, L.J., E.B. Sherr, B.F. Sherr, and R.D. Fallon. 1987. Grazing of ciliated Protozoa on free and particle-attached bacteria. Marine Ecology. Progress Series 38: 125-129.

Alekseev, V.R. 1987. Development of zooplankton and seasonal cycles of crustaceans in whitefish nursery ponds influenced by intensification measures. Sbornik nauchnykh trudov GosNIORKh 264: 20-32 (in Russian).

Alekseev, V.R., and I.I. Potina. 1986. Use of structural indices of zooplankton composition for assessment of planktivorous fish impact. Sbornik nauchnykh trudov GosNIORKh 245: 68-76 (in Russian, English summary).

Aliev, A.R. 1989. Fauna of ciliates in natural water bodies of Azerbaijan. Page 8 in 2 Vsesojuznoe Soveschanije protozoologov. Tezisi. (2nd All-Union Meeting of Protozoologists. Abstracts). Yaroslavl' (in Russian).

Allan, J.P. 1983. Predator-prey relationships in streams. Pages 191-229 in J.R.Barnes and G.W.Minshall, editors. Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

Antipchuk, A.F. 1976. Microbiological studies of fishery ponds (The state of the art and prospects). Gidrobiologicheskij zhurnal 12(2): 91-102 (in Russian).

_____.1983. Mikrobiologia rybovodnykh prudov. (Microbiology of fish farming ponds). Legkaja i pishchevaja promishlennost', Moskva (in Russian).

Antipchuk, A.F., N.N. Kharitonova, and T.G. Litvinova. 1977. Microbiological and hydrochemical indices of the process of mineralization of vital activity products of pond fish. Gidrobiologicheskij zhurnal 13(6): 46-51 (in Russian, English summary).

Archibald, C.P. 1975. Experimental observations of the effect of predation by goldfish (*Carassius auratus*) on the zooplankton of a small saline lake. Journal of the Fisheries Research Board of Canada 32: 1589-1594.

Balushkina, E.V., and G.G. Winberg. 1979. Relation between mass and body size in planktonic animals. Pages 169-171 in G.G.Winberg, editor. Obshchie osnovi izuchenija vodnih ekosistem (General foundations of research into aquatic ecosystems). Nauka, Leningrad (in Russian).

Baranova, L.P., and A.S. Yakovlev. 1989. Diurnal rhythm and diet of fish fry reared in Lake Bolshoy Okunenok. Sbornik nauchnykh trudov GosNIORKh 292: 133-146 (in Russian)

Beaver, J. and T. Crisman. 1982. The trophic response of ciliated protozoans in freshwater lakes. Limnology and Oceanography 27 : 246-253.

_____.1989. The role of ciliated protozoa in pelagic freshwater ecosystems. Microbiological Ecology 17: 111-136.

Beavers, R.A., and R.H. Stavn. 1975. Seasonal changes in diaptomid copepod populations as a function of vertebrate predation. Verhandlungen internationale Vereinigung fur theoretische und Angewandte Limnologie 19: 2966-2975.

Benndorf, J., editor. 1988a. Biomanipulation. Limnologica, Berlin 19: 3-110.

_____.1988b. Objectives and unsolved problems in ecotechnology and biomanipulation: A preface. Limnologica, Berlin 19: 5-8.

_____.1990. Conditions for effective biomanipulation; conclusions derived from whole-lake experiments in Europe. Hydrobiologia 200/201: 187-203.

Bergquist, A.M., S.R. Carpenter, and J.C. Latino. 1985. Shifts in phytoplankton size structure and community composition in the course of grazing by contrasting zooplankton assemblages. Limnology and Oceanography 30: 1037-1045.

Bern, L. 1990. Food choice in some freshwater crustacean zooplankters. Acta Universitatis Upsaliensis: Comprehensive Summaries of Uppsala dissertations from the Faculty of Science 245: 1-15.

Brönmark, C. 1988. Effects of vertebrate predation on freshwater gastropods: an exclosure experiment. Hydrobiologia 169: 363-370.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science (Washington, DC) 150: 28-35.

Carpenter, S.R., editor. 1988. Complex interactions in lake communities. Springler-Verlag, New York e.a.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He, and C.N. von Ende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876.

Dawidowicz, P. and J. Pijanowska. 1984. Population dynamics in cladoceran zooplankton in the presence and absence of fishes. Journal of Plankton Research 6: 953-959.

Dumont, H.J., and G. Balvay. 1979. The dry weight estimate of *Chaoborus flavicans* (Meigen) as a function of length and instars. Hydrobiologia 64: 139-145.

Elser, J.J. and S.R. Carpenter. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. Oecologia 76: 148-154.

Gilbert, J.J. 1989. The effect of Daphnia interference on a natural rotifer and ciliate community: Short-term bottle experiments. Limnology and Oceanography 34: 606-617.

Gulati, R.D., E.H.R.R. Lammens, M.-L. Meijer, and E. van *Donk, editors. 1990. Biomanipulation, tool for water management:* Proceedings of the International Conference, Amsterdam, The Netherlands, 8-11 Aug., 1989 (Developments in Hydrobiology 61). Kluwer Academic Publishers, Dordrecht, Boston, London.

Gvozdev, M.A., and Yu.P. Volkov. 1978. The group of Syabero lakes. Izvestija GosNIORKh 128: 50-71 (in Russian, English summary).

Hayne, D.W., and R.C. Ball. 1956. Benthic productivity as influenced by fish predation. Limnology and Oceanography 1: 162-175.

Hessen, D.O., and J.P. Nilssen. 1986. From phytoplankton to detritus and bacteria: effects of short-term nutrient and fish perturbations in a eutrophic lake. Archiv fur Hydrobiologie 105: 273-284.

Hrbaček, J. 1962. Species composition and the amount of the zooplankton in relation to the fish stock. Rozpravy Ceskoslovenske Akademie Ved 72(10): 1-115.

Hrbaček, J., M. Dvorakova, V. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verhandlungen Internationale Vereinigung fur theoretische und agewandte Limnologie 14: 192-195.

Hurlbert, S.H., J. Zedler, and D. Fairbanks, 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science 175: 639-641.

Kajak, Z. 1977. Factors influencing benthos biomass in shallow lake enviroments. Ekologia Polska 25: 421-429.

Kamlyuk, L.V., V.P. Lyakhnovich, I.T. Astapovich, L.V. Prosyanik, and G.P.Voronina. 1983. Relation between some links of food chains in fish farming ponds. Pages 163-168 in G.G.Winberg, editor. Troficheskie sviazi i ih rol v produktivnosti prirodnih vodojomov. (Trophic relations and their role in productivity of natural water bodies). Zoological Institute, Leningrad (in Russian).

Kerfoot, W.C., and A. Sih, editors. 1987. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, London.

Knoechel, R., and L.B. Holtby. 1986. Cladoceran filtering rate: body length relationships for bacterial and large algal particles. Limnology and Oceanography 31: 195-200.

Krylov, P.I. 1989. Feeding of freshwater predaceous zooplankton. VINITI Information publications. Seria Obschaya ecologiya, Gidrobiologia, Biocenologia, Vol. 7, VINITI Publishers, Moskva (in Russian).

Lammens, E.H.R.R. 1988. Trophic interactions in the hypertrophic lake Tjeukemeer: top-down and bottom-up effects in relation to hydrology, predation, and bioturbation during the period 1974-1985. Limnologica, Berlin 19(1): 81-85.

Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, and impacts. Hydrobiologia 146: 97-167.

Lokot', L.I. 1987. Ekologia infuzori v ozjerah centralnogo Zabajkalja (Ecology of ciliates in lakes of Central Zabaikal'e). Nauka, Novosibirsk (in Russian).

Lyche, A. 1989. Plankton community response to reduction of planktivorous fish populations. A review of 11 case studies. Aqua Fennica 19: 59-66.

Lynch, M. 1979. Predation, competition, and zooplankton

community structure: an experimental study. Limnology and Oceanography 24: 253-272.

Lynch, M., and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community structure. Limnology and Oceanography 26: 86-102.

McQueen, D.G., J.R. Post, and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Science 43: 1571-1581.

Miura, T. 1990. The effects of planktivorous fishes on the plankton community in an eutrophic lake. Hydrobiologia 200/201: 567-579.

Nekrasova, I.I. 1988. Quantitative relation between structural and functional parameters of the zooplankton and pressure of planktivorous fishes introduced into intensively exploited fishery lakes. Sbornik nauchnykh trudov GosNIORKh 283: 74-88 (in Russian, English summary).

Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. Canadian Journal of Fisheries and Aquatic Science 45: 361-379.

Northcote, T.G., C.J. Walters, and J.M.B. Hume. 1978. Initial impacts of fish introductions on the macrozooplankton of small oligotrophic lakes. Verhandlungen Internationale Vereinigung fur theoretische und Angewandte Limnologie 20: 2003-2012.

Opuszynski, K. 1980. The role of fishery management in counteracting eutrophication processes. Pages 263-269 in J.Barica and L.R. Mur, editors. Hypertrophic ecosystems (Developments in Hydrobiology 2). W. Junk bv Publishers, The Hague e.a.

Panov, V.E., A.M. Pavlov, and E.V. Balushkina. 1988. Structure of food webs in invertebrate communities. Pages 165-177 in A.F.Alimov, editor. Communities of freshwater invertebrates in the macrophyte beds. Trudy Zoologicheskogo Instituta AN SSSR 186 (in Russian).

Porter, K.G., E.B. Sherr, B.F. Sherr, M. Pace, and R.W. Sanders. 1985. Protozoans in planktonic food webs. Journal of Protozoology 32: 409-415.

Potina, I.I. 1985. Seasonal increase of the quota of small rotifers in fertilized lakes. Sbornik nauchnykh trudov GosNIORKh 231: 47-52 (in Russian, English summary).

Razumov, A.S. 1932. Direct method for assessment of bacteria in the water. A comparison with Koch method. Mikrobiologija 1(22): 131-146 (in Russian).

Richardson, W.B., S.A. Wickham, and S.T. Threlkeld. 1990. Food web response to the experimental manipulation of a benthivore (*Cyprinus carpio*), zooplanktivore (*Menidia beryllina*) and benthic insects. Archiv fur Hydrobiolie 119: 143-165.

Riemann, B. and M. Sondergaard. 1986. Regulation of bacterial production in two eutrophic lakes and in experimental enclosures. Journal of Plankton Research 8: 519-536.

Romanenko, V. I., and E.G. Dobrynin. 1978. Specific weight of dry biomass in pure bacterial cultures. Mikrobiologija 47(2): 270-272 (in Russian).

Rudenko, G.P., A.S. Pechnikov, and A.S. Yuakovlev. 1989. First results of rearing of large yearlings of carp and coregonid fishes in the nursery lakes in Leningrad district. Sbornik nauchnykh trudov GosNIORKh 292: 21-26 (in Russian).

Schoenberg, S.A., and A.E. Maccubbin. 1985. Relative feeding rates on free and particle-bound bacteria by freshwater macrozooplankton. Limnology and Oceanography 30: 1084-1090.

Shapiro, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. Pages 105-116 in J.Barbica and L.R. Mur, editors. Hypertrophic ecosystems (Developments in Hydrobiology 2). W. Junk bv Publishers, The Hague e. a.

Sibbing, F.A. 1988. Specializations and limitations in the utilization of food resourses by the carp, *Cyprinus carpio*: a study of oral food processing. Environmental Biology of Fish 22: 161-178.

Skoptsov, V.G., and T.V. Krupennikova. 1982. The role of planktivorous fishes in forming lake plankton community structure. Ekologia 5: 41-46 (in Russian).

Spelling, S.M., and J.O. Young. 1987. Predation on lake-dwelling leeches (Annelida, Hirudinea): an evaluation by field experiment. Journal of Animal Ecology 56: 131-146.

Stenson, J.A.E. 1982. Fish impact on rotifer community structure. Hydrobiologia 87: 57-64.

_____.1984. Interactions between pelagic metazoan and protozoan zooplankton, an experimental study. Hydrobiologia 111: 107-112.

Stockner, J.G., and K.G. Porter. 1988. Microbial food webs in freshwater planktonic ecosystems. Pages 69-83 in S.R.Carpenter, editor. Complex interactions in lake communities. Springler-Verlag, New York e.a.

Stone, L. 1990. Phytoplankton-bacteria-protozoa interactions: a qualitative model portraying indirect effects. Marine Ecology. Progress Series 64: 137-145.

Stout, J.D. 1980. The role of protozoa in nutrient cycling and energy flow. Advances of Microbiological Ecology 4: 1-50.

Tatrai, I., L.G. Thoth, J.E. Ponyi, J. Zlinskzky, and V. Istvanovicz. 1990. Bottom-up effects of bream (*Abramis brama* L.) in Lake Balaton. Hydrobiologia 200/201: 167-175.

Telesh, I.V. 1990. Effect of fish addition on the population dynamics of rotifers in the experimental lake. Pages 80-88 in L.A.Kutikova, editor. Rotifers. Trudi III Symposiuma, Leningrad (in Russian).

_____. 1991. Fish impact on planktonic rotifers. Hydrobiologia (in press).

Tereshenkov, I.I., A.E. Korolev, A.S. Pechnikov, and Yu.A. Erofeev. 1987. Results of experiments controlling standarts for culturing fish stocking material in nursery lakes. Sbornik nauchnykh trudov GosNIORKh 264: 116-123 (in Russian, English summary).

Thorpe, J.H., and E.A. Bergey. 1981. Field experiments on responses of a freshwater benthic macroinvertebrate community to vertebrate predators. Ecology 62: 365-375.

van Donk, E., and R.D. Gulati, editors. 1989. Biomanipulation in the Netherlands: applications in freshwater ecosystems and estuarine waters. Hydrobiological Bulletin 23: 1-99.

Vaque, D., C. Marrase, V. Iniguez, and M. Alcaraz. 1989. Zooplankton influence on the phytoplankton-bacterioplankton coupling. Journal of Plankton Research 11: 625-632.

Voronova, G.P. 1985. The role of bacteria in productivity processes in fish farming ponds in Belorussia at different intensity of exploitation. Dissertation, thesis., Moskva (in Russian).

Weglenska, T., K. Dusoge, J. Ejsmont-Karabin, I. Spodniewska, and J. Zachwieja. 1979. Effects of winter-kill and changing fish stock on the biocenosis of the pond-type lake Warniak. Ekologia Polska 27: 39-70.

Winberg, G.G. and G.M. Lavrentyeva, editors. 1982. Metodologicheskie rekomendacii po sboru i obrabotke gidrobiologicheskih dannyh pri issledovanii presnyh vod. Zooplankton i ego produccia. (Methodological recommendations for sampling and treatment of hydrobiological data during the investigations of freshwaters. Zooplankton and its production). Leningrad (in Russian).

Young, J.O., and S.M. Spelling. 1986. The influence of predation on lake-dwelling leeches. Freshwater Biology 16: 465-477.

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press, New Haven, London.

Ziebell, C.D., J.C. Tash, and R. L. Barefield. 1986. Impact of threadfin shad on macrocrustacean zooplankton in two Arizona lakes. Journal of Freshwater Ecology 3: 399-406.

Влияние рыб на структуру, численность и биомассу планктона и бентоса двух мелководных озер: трехлетнее исследование

А.Ф.Алимов, Л.Е.Анохина, Е.В.Балушкина, С.М.Голубков, Т.В.Хлебович, П.И.Крылов, Е.В.Павельева, И.В.Телеш, Л.П.Умнова

Зоологический институт Российской Академии наук, Университетская наб., 1, С.Петербург, 199034, Россия

Сопоставлена структура, динамика численности и биомассы планктона и бентоса в двух небольших, близко расположенных мелководных озерах на протяжении летних сезонов 1986-1988 гг. Одно из озер (Малый Окуненок = МО) в 1986-1987 г. было безрыбным, а в 1988 г. в него была посажена молодь карпов. Второе озеро (Большой Окуненок = БО) все три года зарыблялось разными количествами молоди планктоноядных (сиговые) и бентосоядных (карп) рыб. Под действием интенсивного пресса планктоноядных рыб значительно изменилась структура зоо-, фито- и бактериопланктона. В зоопланктоне БО доминировали мелкие виды циклопид (*Thermocyclops, Mesocyclops*) и кладоцер (*Bosmina longirostris, Chydorus sphaericus, Daphnia galeata*); в зоопланктоне МО - более крупные *Daphnia longispina* и личинки *Chaoborus* flavicans. Среди коловраток большую роль в БО играла *Asplanchna priodonta*, встречавшаяся в МО единично. Среди инфузорий, доминировавших в планктоне БО И МО, не встречено ни одного общего вида. Доля бактерий, ассоциированных с частицами детрита в БО была выше, чем в МО. Летнее "цветение" воды в МО было обусловлено массовым развитием *Anabaena spiroides*, в то время как в фитопланктоне БО доминировали другие виды. Бентосоядные рыбы при высоких плотностях посадки подавляли развитие донных сообществ. Пресс бентосоядных рыб сказался на структуре сообществ бентоса, и приводил, в частности, к снижению доли пиявок в общей биомассе донных животных.

В 1986-1987 гг. сильный пресс рыб в БО приводил к снижению средней за сезон биомассы личинок *Chaoborus* в 19-65 раз, планктонных ракообразных в 2.8-3.5 раза. В этот же период биомасса коловраток в БО была выше в 1.6-2.1 раза, фитопланктона в 1.5-1.6 раза, гетеротрофных бактерий - в 1.8-3.0 раза. Среднее содержание хлорофилла-а в БО было в 1.1-1.6 раз выше, а прозрачность воды по диску Секки в 1.3-1.9 раз ниже, чем в МО. По наблюдениям в 1988 г. прослежено непрямое влияние бентосоядных рыб на компоненты пелагической пищевой цепи. Обсуждаются возможные механизмы прямого и опосредованного влияния рыб на сезонную динамику планктона и бентоса.

Appendix 1. Mean monthly zooplankton abundance in BO in 1986-1988: numbers (N, ind/l), biomass (B, mg/l) and no. samples per month (n).

Year	Month	n	Copepoda						Cladocera							
			Nauplii		Cyclopidae		Diaptomidae		*Daphnia*		*Bosmina*		Other Cladocera		*Chaoborus*	
			N	B	N	B	N	B	N	B	N	B	N	B	N	B
1986	May	2	26.37	0.034	28.58	0.415	1.38	0.035	0.45	0.010	0.03	0	0.15	0.001	0.05	0.001
	Jun	2	174.63	0.180	97.39	0.963	6.43	0.338	16.36	0.497	0.06	0	0.16	0.003	0.66	0.084
	Jul	3	19.03	0.025	219.58	1.911	4.12	0.203	18.36	0.365	12.11	0.026	0.52	0.022	0.04	0.001
	Aug	3	5.05	0.007	167.63	1.174	0.22	0.012	8.63	0.166	18.39	0.040	1.01	0.033	0.04	0.002
	Sep	2	22.22	0.034	139.26	0.862	0.04	0.001	9.10	0.177	32.46	0.075	0.97	0.007	0.07	0.005
	Oct	1	4.81	0.007	29.61	0.258	0.04	0.002	11.54	0.259	52.54	0.142	8.97	0.055	0	0
	Nov	2	0.70	0.001	7.62	0.308	0	0	9.81	0.256	55.72	0.254	17.43	0.086	0	0
1987	May	5	51.76	0.067	112.66	2.340	0	0	0.22	0.005	2.31	0.012	0.26	0.001	—	—
	Jun	9	33.29	0.043	67.89	0.967	0.02	0	11.72	0.364	96.65	0.467	8.47	0.051	—	—
	Jul	8	100.07	0.130	194.34	0.972	0	0	1.71	0.037	128.19	0.480	1.76	0.048	—	—
	Aug	4	18.22	0.024	36.26	0.201	0	0	0.14	0.002	18.78	0.060	0.05	0.016	—	—
	Sep	1	6.61	0.009	6.92	0.042	0	0	0.06	0.001	87.84	0.306	0.125	0.001	—	—
1988	May	5	31.16	0.041	88.14	1.275	0	0	0.62	0.030	1.41	0.003	0.22	0.002	0.44	0.094
	Jun	7	12.13	0.016	38.92	0.510	0.02	0.001	21.08	0.814	8.67	0.018	0.12	0.001	0.99	0.304
	Jul	7	12.98	0.017	81.83	0.724	0.02	0.001	5.23	0.179	9.25	0.019	0.19	0.001	0.02	0.002
	Aug	6	5.86	0.008	79.52	0.554	0	0	0.13	0.006	0.24	0	0.04	0	0.13	0.018
	Sep	4	3.57	0.005	35.72	0.191	0	0	0.09	0.006	0.60	0.001	0.01	0	0.01	0.001

Appendix 2. Mean monthly zooplankton abundance in Mo in 1986-1988 (N, ind/l), biomass (B, mg/l), and no. samples per month (n).

Year	Month	n	*Daphnia* spp.		Other Crustacea		*Chaoborus*	
			N	B	N	B	N	B
1986	May	2	9.58	0.771	16.91	0.138	0.22	0.193
	Jun	4	47.09	6.355	30.44	0.127	1.68	1.601
	Jul	4	93.86	10.746	13.61	0.054	2.53	1.612
	Aug	3	51.53	5.663	7.60	0.038	2.62	1.401
	Sep	2	29.67	1.776	7.96	0.033	1.78	1.756
	Oct	1	1.52	0.199	1.96	0.014	1.42	2.204
	Nov	2	0.13	0.041	2.44	0.093	0.92	1.817
1987	May	5	29.77	2.701	20.18	0.147	0.62	1.544
	Jun	10	91.27	6.133	14.37	0.179	1.81	0.469
	Jul	8	29.62	1.967	10.54	0.134	3.50	1.701
	Aug	4	42.26	4.976	5.04	0.094	1.61	1.451
	Sep	2	9.36	2.374	2.82	0.029	1.49	1.264
1988	May	5	26.79	2.154	23.34	0.083	1.09	2.773
	Jun	8	37.20	4.809	6.43	0.050	4.83	1.387
	Jul	7	19.17	2.110	3.83	0.032	3.11	1.480
	Aug	6	3.772	3.950	3.86	0.034	1.40	1.218
	Sep	4	44.00	5.068	2.64	0.023	0.50	0.503

Appendix 3. Mean monthly abundance of small rotifers in BO and MO in 1986-1988: numbers (N, 10^3/L) and biomass (B, mg/L)

Year	Month	BO		MO	
		N	B	N	B
1986	May	9.72	8.1	1.32	1.3
	Jun	4.27	2.2	9.17	10.7
	Jul	8.48	6.6	1.85	4.4
	Aug	3.72	4.2	2.40	3.2
	Sep	1.48	1.7	1.26	1.1
	Oct	2.54	2.1	0.99	0.6
	Nov	0.64	0.2	1.48	1.0
1987	May	1.83	1.8	5.42	4.2
	Jun	5.36	4.7	2.28	2.6
	Jul	10.10	13.8	6.15	6.6
	Aug	11.63	8.6	26.90	6.4
	Sep	5.02	5.6	2.31	1.4
	Oct	5.45	3.8	1.80	2.4
1988	May	0.34	0.2	1.39	0.9
	Jun	10.17	4.7	9.42	6.4
	Jul	5.48	3.5	3.46	6.2
	Aug	2.16	1.6	7.43	10.3
	Sep	7.34	4.7	8.55	4.6
	Oct	3.65	2.3	6.57	3.0
	Nov	0.27	0.2	3.01	3.3

Appendix 4. The ciliate taxa found in plankton of MO and BO during summer seasons 1986-1988.Mean monthly abundance of small rotifers in BO and MO in 1986-1988:

Taxa	BO	MO
Loxodes rostrum O.F.Mull.	—	+
Holophrya atra Svec.	+	+
H.nigricans Laut.	+	+
Bursella spumosa Schmidt	+	+
Prorodon ovum (Ehrb.) Kahl	—	+
Urotricha pelagica Kahl	—	+
Coleps hirtus Nitzsch.	+	—
C.hirtus var. *viridis* Ehrb.	+	—
Enchelys pupa (O.F.Mull.) Ehrb—Schew.	+	+
Lacrymaria olor O.F.Mull.	+	—
Dileptus anser O.F.Mull.	+	—
D.cygnus Clap. et L.	+	—
Paradileptus elephantinus Svec.	+	+
Trachelius ovum Ehrb.	+	—
Cyclotrichium limneticum Kahl	—	+
Didinium balbiani Fabre—Dom.	+	+
D.balbiani var. *rostratum* Kahl	—	+
D.nasutum O.F.Mull.	—	+
Actinobolina vorax Wenrich	+	+
A.radians Stein	+	+
Lionotus cygnus O.F.Mull.	—	+
Phascolodon vorticella Stein	+	—
Colpidium colpoda Ehrb.	+	+
Paramecium bursaria (Ehrb.) Focke	+	—
Frontonia leucas Ehrb.	—	+
Urocentrum turbo O.F.Mull.	—	+
Stokesia vernalis (Wang) Wenzich	+	—
Lembadion bullinum Maskell	+	+
Vorticella anabaena Still	+	+
V.convallaria L.	+	+
V.mayeri Faure—Fremiet	+	+
Epistylis rotans Svec.	+	—
Spirostomum minus Roux	+	+
S.ambiguum Mull.—Ehrb.	—	+
Condylostoma vorticella Ehrb.	—	+
Stentor coeruleus Ehrb.	—	+
St.roeseli Ehrb.	+	+
Bursaridium sp.	—	+
Halteria grandinella O.F.Mull.	—	+
Meseres cordiformis Schew.	+	—
Strombidium mirabile Penard	+	+
St.viride Stein	+	—
St.viride f. *pelagica* Kahl	—	+
Strobilidium velox Faure—Fr.	+	+
Tintinnidium fluviatile Stein	+	+
Codonella cratera Leidy	+	—
Stichotricha aculeata Wrzen.	+	—
Hypotrichidium conicum Slow	—	+
Strongylidium lanceolatum Kowal.	+	+
Urostyla grandis Ehrb.	—	+
Uroleptus piscis (Mull.) Stein	+	+
Stylonychia mytilus Ehrb.	+	+
Oxytricha sp.	+	—

Appendix 5. Mean monthly phytoplankton biomass (B_p, mg/L), chlorophyll-a content (Chl, μg/L), and Secchi depth (SD, m) in BO and MO during seasons 1986-1988. No. of measurements in parenthesis.

Year	Month	BO			MO		
		B	Chl	SD	B	Chl	SD
1986	May	48.6 (2)	110.2 (2)	0.75 (2)	1.7(2)	33.5 (2)	1.10 (2)
	Jun	14.7 (2)	60.7 (3)	0.65 (3)	19.9(2)	82.6 (3)	0.77 (3)
	Jul	35.4 (3)	80.4 (10)	0.51 (7)	30.9 (3)	123.2 (8)	1.14 (5)
	Aug	19.6 (3)	94.8 (4)	0.49 (4)	7.2 (3)	50.0 (4)	1.00 (4)
	Sep	15.3 (3)	144.1 (2)	0.50 (2)	22.2 (3)	21.1 (2)	1.45 (2)
	Oct	19.4 (1)	93.8 (1)	0.56 (1)	3.3 (1)	14.0 (1)	1.25 (1)
	Nov	22.5 (2)	110.4 (2)	0.54 (2)	2.7 (2)	41.4 (2)	1.40 (2)
1987	May	4.6 (4)	69.7 (4)	0.77 (4)	6.9 (4)	23.6 (4)	1.28 (4)
	Jun	12.1 (5)	26.4 (5)	1.25 (5)	10.3 (5)	32.3 (5)	1.25 (5)
	Jul	8.4 (6)	39.8 (11)	0.91 (11)	7.4 (6)	72.2 (12)	1.04 (12)
	Aug	9.6 (3)	26.6 (13)	0.96 (10)	1.6 (3)	26.6 (12)	1.20 (10)
	Sep	28.8 (2)	37.2 (4)	0.89 (3)	14.6 (2)	25.2 (3)	1.31 (3)
	Oct	12.4 (2)	21.8 (2)	1.27 (2)	9.0 (2)	30.6 (2)	1.17 (2)
1988	May	7.8 (5)	7.0 (3)	1.24 (2)	8.9 (5)	24.1 (3)	1.06 (2)
	Jun	5.1 (3)	9.6 (6)	1.50 (6)	10.5 (3)	78.2 (6)	0.62 (6)
	Jul	12.3 (3)	30.4 (13)	1.02 (13)	6.1 (3)	72.9 (13)	0.60 (13)
	Aug	11.7 (3)	30.8 (12)	0.82 (12)	15.8 (3)	141.1 (13)	0.39 (13)
	Sep	12.7 (2)	42.2 (2)	0.81 (2)	4.6 (4)	52.9 (2)	0.92 (2)
	Oct	17.7 (1)	76.0 (1)	0.73 (1)	2.0 (1)	27.3 (1)	1.14 (1)
	Nov	11.0 (1)	48.4 (2)	—	0.3 (1)	12.9 (2)	—

Appendix 6. Mean monthly bacterioplankton abundance values in BO and MO during seasons 1986-1988: numbers (N_b, millions per ml, X ± 1 SD) and no. samples per month (n).

Month	1986			1987			1988		
	n	N_b		n	N		n	N	
		BO	MO		BO	MO		BO	MO
April	1	2.4	7.3	1	3.7	2.5	—	—	—
May	1	4.8	4.0	2	3.95 0.78	2.7±0.14	4	3.4±0.72	2.02±0.63
June	1	8.,8	4.7	5	4.540.78	2.54±0.90	6	4.17±1.53	3.19±0.87
July	2	9.154.45	5.05±3.89	5	6.46±1.60	4.12±0.26	6	3.99±1.15	4.77±1.90
August	3	11.94.35	4.17±2.15	4	4.6±1.35	1.80±0.79	6	6.98±1.29	6.02±2.24
September	2	12.73.11	3.90±1.41	3	5.17±0.38	2.30±0.95	2	5.8±2.51	5.76±2.23
October	1	11.4	2.5	2	4.71.84	2.45±0.78	2	4.6±0.66	6.20±1.35
November	2	5.850.78	4.55±0.64	—	—	—	2	3.30±0.33	3.20±0.44

Appendix 5. Mean monthly phytoplankton biomass (B_p, mg/L), chlorophyll-a content (Chl, μg/L), and Secchi depth (SD, m) in BO and MO during seasons 1986-1988. No. of measurements in parenthesis.

Year	Month	BO			MO		
		B	Chl	SD	B	Chl	SD
1986	May	48.6 (2)	110.2 (2)	0.75 (2)	1.7(2)	33.5 (2)	1.10 (2)
	Jun	14.7 (2)	60.7 (3)	0.65 (3)	19.9(2)	82.6 (3)	0.77 (3)
	Jul	35.4 (3)	80.4 (10)	0.51 (7)	30.9 (3)	123.2 (8)	1.14 (5)
	Aug	19.6 (3)	94.8 (4)	0.49 (4)	7.2 (3)	50.0 (4)	1.00 (4)
	Sep	15.3 (3)	144.1 (2)	0.50 (2)	22.2 (3)	21.1 (2)	1.45 (2)
	Oct	19.4 (1)	93.8 (1)	0.56 (1)	3.3 (1)	14.0 (1)	1.25 (1)
	Nov	22.5 (2)	110.4 (2)	0.54 (2)	2.7 (2)	41.4 (2)	1.40 (2)
1987	May	4.6 (4)	69.7 (4)	0.77 (4)	6.9 (4)	23.6 (4)	1.28 (4)
	Jun	12.1 (5)	26.4 (5)	1.25 (5)	10.3 (5)	32.3 (5)	1.25 (5)
	Jul	8.4 (6)	39.8 (11)	0.91 (11)	7.4 (6)	72.2 (12)	1.04 (12)
	Aug	9.6 (3)	26.6 (13)	0.96 (10)	1.6 (3)	26.6 (12)	1.20 (10)
	Sep	28.8 (2)	37.2 (4)	0.89 (3)	14.6 (2)	25.2 (3)	1.31 (3)
	Oct	12.4 (2)	21.8 (2)	1.27 (2)	9.0 (2)	30.6 (2)	1.17 (2)
1988	May	7.8 (5)	7.0 (3)	1.24 (2)	8.9 (5)	24.1 (3)	1.06 (2)
	Jun	5.1 (3)	9.6 (6)	1.50 (6)	10.5 (3)	78.2 (6)	0.62 (6)
	Jul	12.3 (3)	30.4 (13)	1.02 (13)	6.1 (3)	72.9 (13)	0.60 (13)
	Aug	11.7 (3)	30.8 (12)	0.82 (12)	15.8 (3)	141.1 (13)	0.39 (13)
	Sep	12.7 (2)	42.2 (2)	0.81 (2)	4.6 (4)	52.9 (2)	0.92 (2)
	Oct	17.7 (1)	76.0 (1)	0.73 (1)	2.0 (1)	27.3 (1)	1.14 (1)
	Nov	11.0 (1)	48.4 (2)	—	0.3 (1)	12.9 (2)	—

Appendix 6. Mean monthly bacterioplankton abundance values in BO and MO during seasons 1986-1988: numbers (N_b, *millions per ml, X ± 1 SD) and no. samples per month (n).*

Month	1986			1987			1988	
	n	N_b		n	N		N	
		BO	MO		BO	MO	BO	MO
April	1	2.4	7.3	1	3.7	2.5	—	—
May	1	4.8	4.0	2	3.95 0.78	2.7±0.14	4	3.4±0.72 2.02±0.63
June	1	8.,8	4.7	5	4.540.78	2.54±0.90	6	4.17±1.53 3.19±0.87
July	2	9.154.45	5.05±3.89	5	6.46±1.60	4.12±0.26	6	3.99±1.15 4.77±1.90
August	3	11.94.35	4.17±2.15	4	4.6±1.35	1.80±0.79	6	6.98±1.29 6.02±2.24
September	2	12.73.11	3.90±1.41	3	5.17±0.38	2.30±0.95	2	5.8±2.51 5.76±2.23
October	1	11.4	2.5	2	4.71.84	2.45±0.78	2	4.6±0.66 6.20±1.35
November	2	5.850.78	4.55±0.64	—	—	—	2	3.30±0.33 3.20±0.44